ECOLOGY OF NOTHOFAGUS SOLANDRI

(Black beech and Mountain beech)

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by

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CONTENTS

SECTION 1 INTRODUCTION

1.1. AIM OF STUDY

The species Nothofagus solandri, within which two subspecific taxa are recognised, i.e. Nothofagus solandri var. solandri and Nothofagus solandri var. cliffortioides (for descriptions see below), occupies a wide geographical and ecological range throughout much of New Zealand. It is often the only tree species of any account throughout the headwaters of many of New Zealand's larger rivers, especially those which have their origins on the eastern side of the Main Divide in the South Island and in the central mountain ranges of the North Island. For this reason the species is one of our most important protection forest trees and the forests which it forms must be kept in a healthy regenerating condition in order that they effectively act as a barrier to excessive soil erosion and minimise fluctuations in water yield. To fulfill these requirements and thus to aid in the management of these forests, some knowledge of the ecological behaviour, the life history, and variations in the life history of Nothofagus solandri is necessary.

The aim of this thesis is to investigate the life history and ecological behaviour of Nothofagus solandri, to relate variations in the life history to habitat and thus to attempt to explain the present geographic and ecological distribution of the species.

During the course of this study many of the forests of which Nothofagus solandri is a component were visited, but detailed experimental work was mainly confined to the Craigieburn Range and

Mt Thomas in North Canterbury and the Kaweka Range in the Central North Island.

1.2. DESCRIPTION OF SPECIES

The following descriptions of the two taxa are taken from Allan, 1961, pp 399-400 except for sections which I have interpolated and which are underlined.

Nothofagus solandri (Hook. f.) Oerst. (~~Black beech~~).

var. solandri (Black beech)

Evergreen tree up to 27 m. tall; trunk up to 1 m. or more diam. Leaves alternate, coriaceous, 10-15 x 5-10 mm., on petioles 1-2 mm. long; lamina narrow-oblong to elliptic-oblong, obtuse, obliquely cuneate at base, often apiculate; glabrous or nearly so above, clad in dense greyish white tomentum below; venation usually distinct on both surfaces. Domatia absent. Monoecious. Staminate inflorescences 1-4 per branchlet, on short, sparsely pubescent peduncles; flowers 1-2, sessile. Perianth broad-campanulate, 2 x 3 mm., shallowly, obtusely 4-5 lobed; stamens 8-17, anthers 2-3 mm. long, dark red. Pistillate inflorescences ovoid, 1-2 per branchlet, pubescent-pilose, sessile; flowers 1-3. Lateral flowers trimerous, terminal dimerous; stigmas clavate. Cupule 6-7 mm. long, glabrous to pubescent, 3-partite. Nuts up to 7 mm. long; wings broad at base, narrowed to apex.

Wood pinkish to yellowish, often with darker patches; bark of young trees pale and smooth, of older trees rough, furrowed, very dark. Juvenile plants often of semi-divaricating habit with broadly ovate-oblong, reddish leaves 5-7 x 4.5 mm.

var. cliffortioides (Hook. f.) Poole. (Mountain beech)

Evergreen tree up to 27 m. tall; trunk up to 1 m. or more diam.; often reduced to shrub on harsh sites. Leaves alternate coriaceous, 10-15 x 7-10 mm., on petioles 1-2 mm. long; lamina ovate to ovate-oblong, acute to subacute, obliquely rounded at base, often glabrous but occasionally lightly pubescent above, clad in dense, greyish-white to subfulvous tomentum below; nervation usually obscure. Domatia absent. Monoecious. Staminate inflorescences 1-3 per branchlet, 1-2 flowered; peduncles very short, sparsely pubescent. Perianth broadly campanulate, 2 x 2 mm., with 4-5 obtuse lobes. Stamens 8-14; anthers 2-3 mm. long, dark red. Pistillate inflorescences 1-(2) per branchlet, sessile, viscous, almost glabrous to pubescent, 2 mm. long. Lateral flowers trimerous, terminal dimerous; stigmas clavate. Cupule 3-partite, up to 7 mm. long. Nuts glabrous to puberulous, 6-7 mm. long; wings with acute tips.

Wood usually paler than that of N. solandri. Bark rather smooth, dark. Juvenile plants have strong apical dominance and have ovate to suborbicular leaves 4-7 x 4-5 mm.

1.3. PROCEDURE

The study has been subdivided into three major parts. Each of these parts is dealt with under a separate section heading. The section headings are as follows:-

Section 1: Introduction

Section 2: The distribution of mountain beech and black beech in relation to other forest and scrub species.

Section 3: The mountain and black beech associations.

Section 4: The life history and behaviour of Nothofagus solandri.

Section 5: Discussion.

In Section 2, the distribution of mountain beech and black beech is discussed. An attempt has been made to relate the distribution of the species to locality, altitude, soil moisture, parent rock, and other features of the habitat, and to record the major species of the vegetation which replace it.

In Section 3 an attempt is made to describe, define and subdivide the range of habitat of mountain beech and black beech by a quantitative plant socialogical analysis. Each association (floristic unit derived by the application of this analysis) is defined in terms of species composition and of recognisable habitat factors.

In Section 4 the results are given for studies on the flowering, seeding, germination, early seedling development and mortality, phenology, tree growth and mortality and stand growth of Nothofagus solandri. Where information is available variation in the life history is related to changes in site. Examples are given showing how the pattern of behaviour may change from one association to another.

In Section 5 an attempt is made to explain the present geographic and ecological distribution of the species in terms of its life history. The application of the results of the study to the management of the Nothofagus solandri forests is discussed.

SECTION 2 THE DISTRIBUTION OF MOUNTAIN AND BLACK BEECH IN RELATIONSHIP TO OTHER MAJOR FOREST AND SCRUB SPECIES

2.1. INTRODUCTION

In this section, the part played by mountain beech and black beech in the forests and scrublands of New Zealand is discussed. The distribution of the species has been mapped (see Figs. 1 and 2) while in the text the distribution of each of the two varieties and of intermediate forms is discussed. Some attempt is made to define broadly the limits of altitude, rainfall, soil moisture, plant competition, etc., and other factors of the habitat, for Nothofagus solandri and the major canopy species of the vegetation which replaces mountain beech or black beech under certain conditions is indicated.

The forests and scrublands containing mountain or black beech and the vegetation adjacent to these forests and scrublands will be described locality by locality throughout the country. For convenience, in this description, the country has been divided into four areas (see Locality Maps 1-4): the 'North Island', the 'Northern and Western South Island', the 'Eastern South Island' and the 'Southern South Island'. The 'North Island' includes the area from Cook Strait northwards to the most northern limits of distribution of black beech and mountain beech. The 'Northern and Western South Island' includes the area to the west of the Main Divide and northwest of the Wairau River, from the Taramakau River to Farewell Spit

and the Marlborough Sounds. The 'Eastern South Island' includes the area in the South Island, south of the Wairau River, north of the Waitaki River catchment and to the east of the Main Divide. The 'Southern South Island' contains everything from the Waitaki and Waita catchments southwards.

Information for this section comes largely from my own notes and from ecological plots established by the New Zealand Forest Service. Published descriptions of areas have been used to supplement my own observations and to provide information for some areas I have not visited. In such cases reference is made to the published article. Some of the information arises out of discussion and here when statements are attributable to an individual, acknowledgement is made.

2.2. DESCRIPTION OF THE FORESTS

2.2.1. North Island

The most northerly natural occurrence of both mountain beech and black beech is in the Raukumara Range, East Cape district. Mountain beech is restricted to occasional spurs and knobs in the vicinity of the upper bushline* from Mt Hikurangi southwards. Here it codominates with silver beech (Nothofagus menziesii) but, in general, silver beech is the only large tree species in the upper forests and forms a bushline at between 4550 feet and 4730 feet altitude. Above this level there is a fairly dense scrub belt of Olearia colensoi, Dacrydium biforme, Hebe species and Phyllocladus alpinus. This pattern of distribution of mountain beech and silver

* The term bushline used throughout this thesis is synonymous with timber line as defined by P. Wardle, 1964, p.113 and is the upper limit of tall, erect "timber-sized" trees.

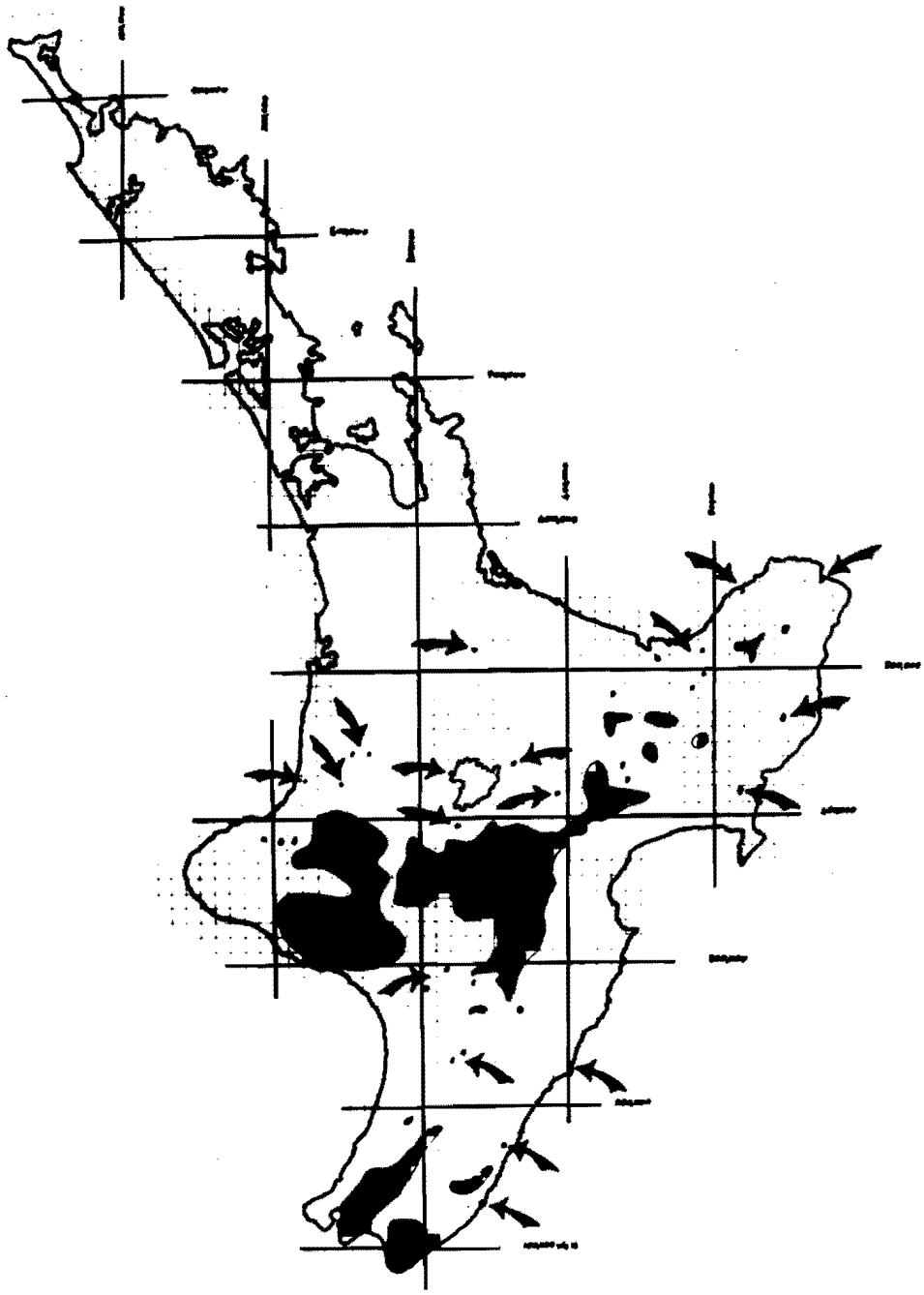


Fig. 1 - Distribution of Nothofagus solandri in North Island. Grid lines are spaced at 100,000-yard intervals, and bear the numbers of the National Grid as they appear on the N.Z.M.S. Maps. The map is then further subdivided into 10,000-yard grid squares.

A boundary to the distribution of the species has been tentatively drawn and within this boundary each 10,000-yard grid square, for which there is a reliable report of occurrence, is blocked in. Isolated occurrences are indicated by arrows.

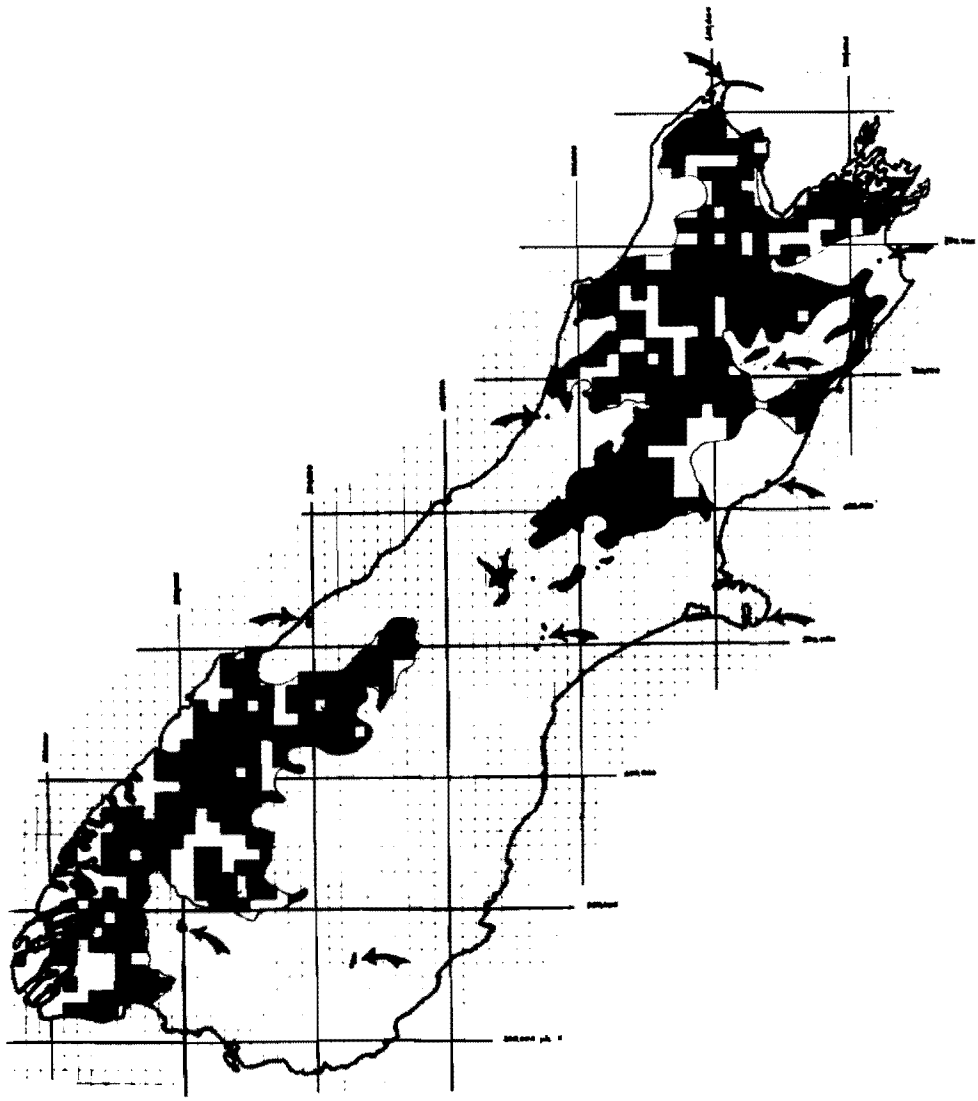
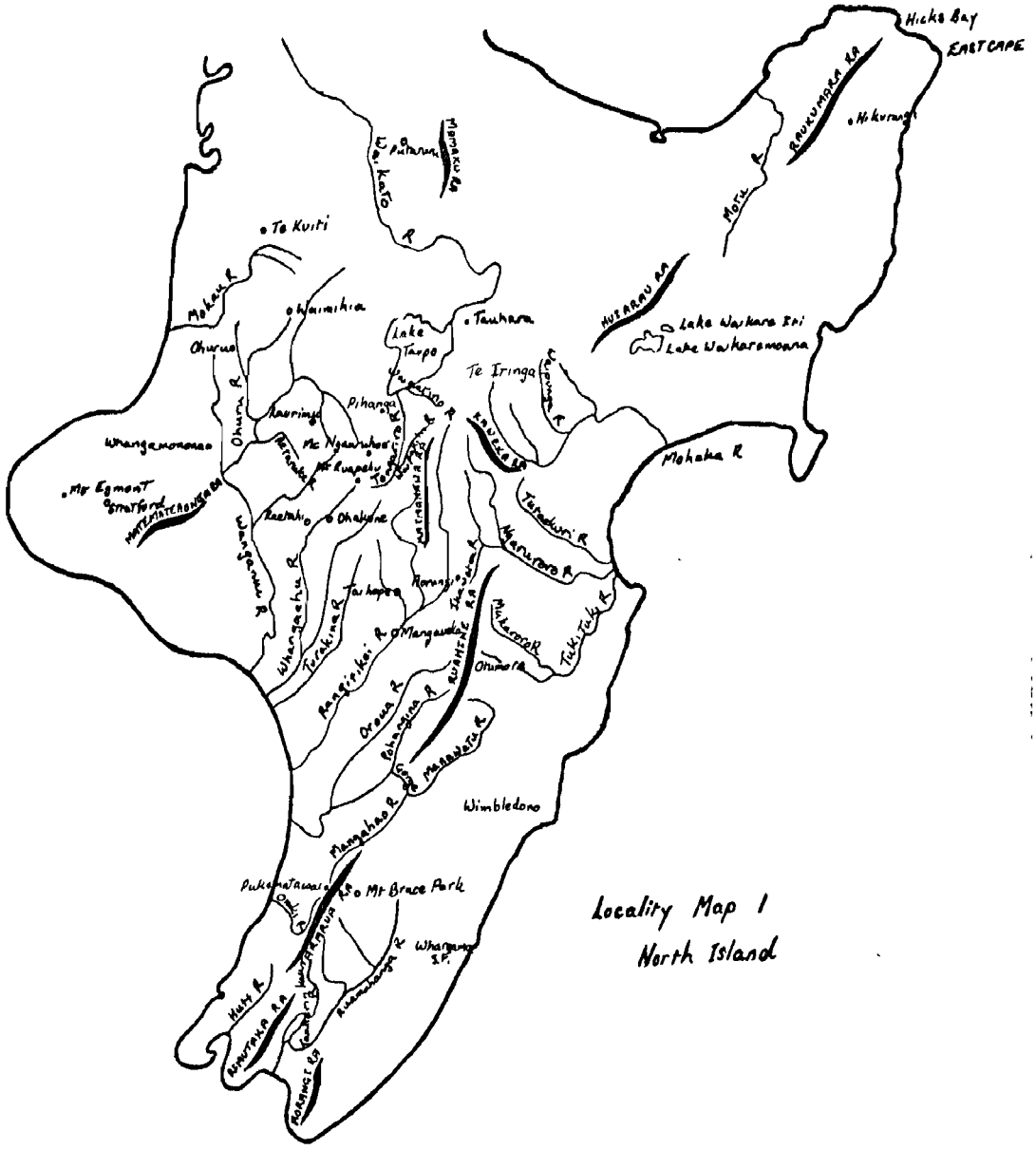


Fig. 2 - Distribution of Nothofagus solandri in South Island. Grid lines, distributional boundaries, and definite occurrences of the species marked as for Fig. 1.

beech persists throughout the Raukumara and Northern Huiarau Ranges to at least as far south as Lake Waikaremoana. However, on one swampy area not far north of Lake Waikare-iti, mountain beech does occur at 3000 feet altitude together with Dacrydium colensoi.

Scattered stands of black beech occur below 3000 feet on spur sites in what is predominantly a podocarp forest belt, to as far north as Hicks Bay. These stands are rare close to the Main Divide but become more common in the foothills in both the east and the west and in the east some stands extend almost to the coast. In these northern stands, black beech is almost invariably associated with tawa, (Beilschmiedia tawa), kamahi (Weinmannia racemosa), and rewarewa (Knightia excelsa) and often also with rimu (Dacrydium cupressinum). Sometimes red beech (Nothofagus fusca), and occasionally even pohutukawa (Metrosideros excelsa) may be present, and, particularly towards the north and west, hard beech (Nothofagus truncata) may be associated.

There is a tendency for silver beech to diminish in importance in these communities on moving south from Lake Waikaremoana towards the Mohaka River and west towards the Waipunga River. This is paralleled by an increase in the importance of mountain beech. Mountain beech becomes more general towards the bushline and also descends to progressively lower altitudes. In the extreme south-west it may occasionally occur on old fire scars, steep slopes and spurs at altitudes below 2000 feet in what is predominantly a red beech - podocarp forest. At these low altitudes there is a distributional overlap with black beech and forms intermediate between the two are common.



To the west of the Waipunga River the forest cover in the northern tributaries of the Mohaka River is largely discontinuous and much of the area is covered by Leptospermum scrub. The forest which does remain usually includes podocarp species and red beech, with silver beech at higher altitudes. Mountain beech occurs only as rare and isolated stands on ridge tops and spurs between 2000 feet and 3000 feet altitude in the middle and lower reaches of the tributaries. However, one isolated stand does occur well to the

north, on the summit of Mt Tauhara near Taupo. Here mountain beech forms a small pure stand between 3000 feet and 3300 feet altitude.

Towards the headwaters of the Mohaka River, silver beech may still form the bushline in the southern tributaries but in general the Mohaka River provides a boundary between the predominantly silver beech dominant high altitude forests in the north and the predominantly mountain beech dominant forests in the south. Silver beech occurs to a limited extent in the ultimate headwaters of the Rangitikei and Ngaruroro catchments but further downstream mountain beech replaces it, firstly at the bushline and then at the lower levels. The forest becomes one containing pure mountain beech between 3700 feet and the bushline which is between 4500 feet and 4700 feet. Above bushline there is a sparse scrub zone of Coprosma pseudocuneata, Podocarpus nivalis and Phyllocladus alpinus, and below 3700 feet red beech becomes progressively more important and mountain beech less important in forest composition. Further downstream in the Mohaka valley, in the catchments which drain the eastern flanks of the Kaweka Range, mountain beech is the only large tree species in the upper forest but again it is replaced by red beech below 3700 feet.

In the southern Kaweka Range and in the adjacent stretch of the Rangitikei catchment, the forest cover becomes more discontinuous. In the east, large areas of what must have originally been mountain beech and red beech forests have been cleared by fire and the forest has now been replaced by Leptospermum scrubland, and the small patches which do remain are often confined to gullies. To the west,

at the southern end of the Kaimanawa Range, the forest is largely replaced by tussock, usually red tussock (Chionochloa rubra), and the islands of mountain beech and red beech are replaced by islands of mountain cedar (Libocedrus bidwillii) and halls totara (Podocarpus hallii). After the appearance of cedar, the mountain beech tends to be confined first of all to the forest edges but soon disappears completely.

Trees which may undoubtedly be ascribed to black beech do not occur upstream from the Waipunga confluence in the Mohaka drainage, nor do they occur in the Kaweka or Kaimanawa Ranges, but at low altitudes in all three areas there are some stands of mountain beech which have a strong similarity to black beech in leaf shape.

Still further west, in the Tongariro River headwaters, forest is restricted to ribbons in the vicinity of stream channels and the main vegetation is a tussock grassland dominated by fescue (Festuca spp.) and red tussock. Mountain beech persists as the main tree species but occasionally silver beech of poor form and red beech also occur. On moving downstream towards the Waipakihi River, forest becomes more discontinuous. The forest between 3700 feet and the bushline which is around 4500 feet altitude consists of pure mountain beech but below 3700 feet red beech appears and it codominates with mountain beech at the lower levels. Silver beech occurs near the Waipakihi-Tongariro confluence but only at altitudes below 3500 feet, and Elder (1962) reports that a single tree of Dacrydium colensoi and a log of mountain cedar has also been found in this vicinity. Further downstream in the Tongariro valley a podocarp element appears and becomes increasingly common on moving north.

Mountain beech with some red beech and occasional pockets of silver beech continues to form ribbons along creeks draining into the Tongariro River from the eastern slopes of Mt Ngauruhoe, but after leaving the slopes of Ngauruhoe there is a gap in the distribution of mountain beech until Pihanga Mountain is reached. Here, according to McKelvey (1963), mountain beech occurs as pockets between 3000 feet and 3500 feet, in red beech - silver beech forest, on the north and west slopes of the mountain but most of the area, at least below 2800 feet altitude, is dominated by podocarp species.

On the eastern side of the lower Tongariro River, podocarp species again dominate the lower forest to the exclusion of the beech species. However, from 3000 feet to 3700 feet there is a red beech belt and above this, up to the bushline of 4400 feet to 4500 feet, mountain beech is the sole dominant. Above bushline, mountain beech gives way to a subalpine scrub of Phyllocladus alpinus. However, the Waimarino River forms an eastern boundary for the distribution of mountain beech and further to the east, around Mt Te Iringa, silver and red beech codominate the forest.

On the south- and west-facing slopes of Mt Ruapehu, the Nothofagus solandri forest becomes much more complex, especially towards the west, and the bushline becomes much higher. Whereas in the Waipakihi-Tongariro area the bushline is between 4400 feet and 4500 feet altitude, on the southern and western slopes of Mt Ruapehu it is between 4800 feet and 4950 feet and is thus the highest bushline in the whole of the North Island. Mountain beech is the only tree species at bushline but becomes associated with Dacrydium biforme and mountain cedar below 4600 feet. On the south side of the

mountain, silver beech is also important below 4000 feet and from 4000 feet down to about 3600 feet the forest often consists of combinations of mountain beech and silver beech. Red beech is present below 3600 feet and it codominates in the forest on these lower slopes with silver beech. Mountain beech becomes restricted to the sides of streams, steep faces and areas of poor drainage, and below 2500 feet scattered stands of black beech may take the place of mountain beech. On the west side of the mountain, red beech and silver beech do not form this distinct forest belt. Rather they tend to be restricted to pockets at around 3000 feet altitude and mountain beech is the main tree down to 3200 feet. Below 3200 feet rimu and associated scrub hardwood species such as kamahi and wineberry (Aristotelia serrata) attain dominance.

Below 3500 feet on the western side of Mt Ruapehu are large areas where the soil drainage is poor and on these sites mountain beech and black beech form an important component of the forest. The composition of the forest changes considerably with changes in the degree of freedom of drainage. On the very wettest sites are areas of open pakihi* supporting a herbaceous vegetation dominated by Gleichenia species. With improvement in drainage, first of all Dacrydium bidwillii, Dacrydium colensoi, Dracophyllum subulatum and Phyllocladus alpinus appear and then also mountain beech, black beech, mountain cedar, Dacrydium biforme, halls totara and Leptospermum species. With better drainage still, at least below 3200 feet, the beech forest gradually gives way to podocarp and podocarp-scrub

* Pakihi refers to areas of poorly drained peaty soil.

hardwood forests. These pakihi forests extend westwards to as far as a line joining Raetihi and Raurimu and there is then a gap in the distribution of Nothofagus solandri until the Wanganui River forests are reached.

The forests of the lower and middle Wanganui River are on low-lying but broken mudstone and limestone country. They are dominated by podocarp species and tawa but with the exception of an area surrounding the Matemateaonga Range, black beech occupies the razor back ridges and spurs throughout to within 6 to 8 miles of Stratford. The black beech is in most cases associated with kamahi, rewarewa and tawa, and on the sharpest ridge crests, with northern rata (Metrosideros robusta). Halls totara, rimu and miro (Podocarpus ferrugineus) are often present and, from Whangamomona northwards hard beech is frequently codominant with black beech. In one area, in the lower Retaruke Catchment, silver beech occurs with black beech and hard beech but apart from this local occurrence and one other known occurrence some distance further south, silver beech and also red beech are absent.

Both mountain beech and black beech are absent from the slopes of Mt Egmont and the forest consists of tawa and podocarps at low altitudes and hall's totara and kamahi higher up.

The effective northern limit of black beech in the Wanganui forests is about ten miles to the north of the Wanganui-Ohura River confluence. Further north there are rare stands on spurs but the forest consists predominantly of tawa and podocarp species. One such stand of black beech is located about four miles to the north of Ohura in the vicinity of the lower Mokau River. Another occurs

Fig. 3 - Forest in the Lower Wanganui catchment. Black beech is restricted to narrow stands along the sharper spurs and ridges.

further inland towards Waimihia and yet another about 20 miles due south of Te Kuiti. McKelvey (1963) records black beech on an ignimbrite cliff in the western bay of Lake Taupo and there is a further isolated stand in the Mamaku Range about 10 miles due west of Putaruru in what is again predominantly a tawa forest (J. Nicholls, pers. comm.).

South-east of the Wanganui River and towards the Ruahine Range, the forest has largely been cleared and the former patterns of distribution are hard to reconstruct. Dense stands of podocarps dominate most forest remnants and in the Taihape-Mangaweka area the only common hardwood species of any size is maire (Gymnelaea spp.) (J. Nicholls, pers. comm.). South of Mangaweka, in the Rangitikei

catchment, however, some tawa and rewarewa are encountered. Black beech occurs in forest remnants in the lower Wangaehu valley and probably also in the lower Tarakina valley, and south of Mangaweka, in the Rangitikei valley, there are isolated stands on sharp spurs and terrace rims. To the south, in the mid Oroua and Pohangina catchments, in the foothills of the Ruahine Range, black beech becomes abundant though it is still limited to spur and terrace sites. Here it is usually associated with rimu and often with kahikatea (Podocarpus dacrydioides), red beech, silver beech, tawa, and northern rata.

The forests of the Ruahine Range north of Aorangi Peak are dominated by either mountain cedar, red beech, or mountain beech, though scattered stands of podocarps do occur at low altitudes along the fringes of the range and below 3000 feet there are small stands of black beech on some of the ridges. Much of this lower forest has been cleared however, and, towards the north, the main vegetation is red tussock. The mountain cedar forests are restricted to the vicinity of Aorangi. Red beech forest is only important in the upper Ikawetea valley and below 3600 feet along the eastern fringe of the northern Ruahines. Elsewhere, mountain beech is the main forest tree species. Mountain beech may occur up to 4500 feet but at these upper levels its distribution is restricted to the areas of better drainage. In the large areas of poor drainage and deep peat formation which do occur, mountain beech is replaced by Dacrydium biforme, red tussock and bogs containing sphagnum moss. At the head of the Ikawetea River, Olearia colensoi may form a subalpine scrub belt above the mountain beech but elsewhere mountain beech abuts directly onto tussock.

On moving south from Aorangi, on the western side of the Ruahine Range, the mountain beech forest becomes progressively more restricted to the vicinity of the Main Divide and near the Oroua River headwaters it fades out entirely. The bushline also becomes depressed. In the north, mountain beech may occur up to an altitude of 4700 feet but near the Oroua headwaters the upper limits are probably little more than 4000 feet. The upper mountain beech bushlines are characteristically discontinuous. The stands between 4500 feet and 4700 feet consist of groups of old, open-canopied trees with very little regeneration over a dense Chionochloa understorey and even below 4500 feet the forest is broken, especially in the gullies and seepage spots, by tongues of Olearia colensoi and tussock. Below 3900 feet mountain cedar and Dacrydium biforme are usually present in the mountain beech forest and just south of Aorangi, mountain beech is associated with silver beech in two small stands between 3500 feet and 4000 feet. So far as is known these are the only occurrences of silver beech in the Ruahine Range. Mountain cedar forest is extensive in the vicinity of Aorangi where it usually forms the bushline but further south it mainly becomes restricted to the subsidiary ranges east of the main divide until south of the Oroua River mountain cedar is only present in the form of scattered trees. In the north, Dacrydium biforme is codominant in the mountain cedar forests and the two species usually form a bushline between 3800 feet and 3900 feet but in the south the upper limits of mountain cedar are depressed. Dacrydium biforme maintains its upper limits and the two species tend to become separated with

Dacrydium biforme forming a band above the mountain cedar forest. Both the Dacrydium biforme and the cedar give way to a subalpine scrub of Olearia colensoi.

Fig. 4 - Upper limits of mountain beech in the mid Ruahine Range. The bushlines are characteristically discontinuous and the upper forest consists of groups of old, open-canopied trees, with very little regeneration over a dense Chionochloa understorey. (Photo by N. Elder).

Elder (1965) records that at the ecotone between the mountain beech bushline in the east and the mountain cedar bushlines in the west, the upper limits of mountain beech descend to those of the mountain cedar and at the point of junction pure stands of Dacrydium biforme are often conspicuous.

In the central western Ruahine Range there is a band of red

beech forest between 2000 feet and 3600 feet. It is replaced south of the Oroua River by kamahi forest, and in the north, in the vicinity of Aorangi Peak it is replaced by mountain cedar forest. Mountain beech extends down into this red beech belt to around 3000 feet altitude on the spurs. Below the red beech belt are remnants of what was a podocarp forest prior to land clearing operations. There are stands of black beech on some spurs in this podocarp forest and forms of Nothofagus solandri, intermediate between black beech and mountain beech in leaf characteristics, extend up into the red beech belt. Several small stands of black beech occur between 1500 feet and 2000 feet altitude on the driest sandstone sites in the middle reaches of the Pohangina valley in a forest that is predominantly composed of rimu and northern rata. These are the most southerly stands of Nothofagus solandri in the Ruahine Range, and, according to Elder (1965) they are vestiges of what was once a much more extensive black beech forest capping the long ridge extending between the Oroua and Pohangina valleys.

The pattern of distribution of forest types on the eastern side of the Ruahine Range is much simpler although here again podocarp species and kamahi dominate the forests in the south of the range and above the kamahi are Olearia colensoi and Dacrydium biforme associations. To the north of Otumore Peak is a very abrupt change. Below 2800 feet altitude there is still a scattering of podocarps but the forest up to 3600 feet consists mainly of red beech. Mountain beech forms the bushline at between 4400 feet and 4500 feet altitude but again this bushline is broken by tongues of Chionochloa tussock grassland and Olearia colensoi scrub. The mountain beech ceases to

be an important component of the forest below an altitude of about 3000 feet but on spurs below 2800 feet a form of Nothofagus solandri with strong affinities with black beech often occurs. In the north, towards the Makaroro River these two forms of Nothofagus solandri grade into each other to form extensive forests in which the trees have characteristics intermediate between black and mountain beech.

The most southerly occurrence of Nothofagus solandri on the eastern side of the Ruahine Range is in the headwaters of the Manawatu River. These stands, according to Elder (1965), consist of mountain beech and occur on knolls and spurs between 1600 feet and 3000 feet altitude, and the associate tree species are kamahi, red beech and hall's totara.

South of the Manawatu Gorge, in the Tararua Range and its southern extension, the Rimutaka Range, mountain beech is absent except for one small area in the Mangahao catchment, where four trees with leaf characteristics definitely of mountain beech, were found on the edge of a small pakihi at 1700 feet altitude in a predominantly silver beech, red beech, kamahi forest. With deterioration in drainage, towards the centre of this pakihi, the beech species gave way to Leptospermum scrub.

The bushline forests in the Tararua and Rimutaka Ranges are dominated by silver beech south of Pukematawai Peak and by kamahi to the north. The kamahi bushlines reach altitudes of 2900 feet to 3300 feet near Pukematawai but tend to be depressed further north. Dacrydium biforme is an important element in the upper kamahi forests and above bushline there is a dense subalpine scrub zone of Olearia colensoi and Dracophyllum filifolium. Silver beech, to the south,

forms a bushline between 3000 feet and 3800 feet with an extreme upper limit in the upper Tauherenikau catchment of 3950 feet. Where silver beech is the timberline species, red beech is usually the main forest species below 3000 feet and at altitudes below 2500 feet, rimu, miro, mahoe (Melicytus ramiflorus) and hinau (Elaeocarpus dentatus) become increasingly important in forest composition. Two small patches of black beech occur in the kamahi forests at the extreme northerly tip of the Tararua Range, just south of the Manawatu Gorge, but no more is encountered until the vicinity of Bruce Park is reached. From Bruce Park, southwards, scattered stands extend around the eastern fringes of the range. These stands seldom occur at altitudes above 1700 feet and are generally restricted to spurs and terrace rims within the podocarp forest zone. The only known stands of black beech on the western side of the Tararua Range, north of the Hutt River headwaters, are from the headwaters of the Otaki catchment, and even to the south of the Hutt headwaters black beech probably does not extend as far westwards as the coast and, as far as is known, the Hutt Catchment more or less delineates the western margins of black beech distribution. South of the Hutt and Tauherenikau headwaters black beech becomes a much more important species, particularly on river terraces and spurs up to 1600 feet or 1800 feet altitude, though occasional hybrids between black beech and red beech have been found up to 2500 feet altitude.

The black beech forests are rather similar in composition throughout the Tararua and Rimutaka Ranges. There is usually a podocarp element and the hardwood species, kamahi, hinau and rewarewa

are usually present. There may be some tawa and a few red beech and silver beech, and, in the west hard beech is often present.

Black beech is quite important in the Aorangi Range which is east of the Tararua-Rimutaka mountain complex, and stands of black beech extend northwards up the east coast ranges to at least as far as the Whareama State Forest, and even further north, at Wimbledon on the east coast, there is a record of black beech. Mountain beech is absent from the Aorangi Range and its northern extensions, and silver beech and red beech are the main tree species at high altitudes. Below 1900 feet the forest is generally made up of mahoe, hinau, rewarewa and kanuka (Leptospermum ericoides), but in the north-west corner black beech and hard beech codominate in these lower forests and occur with equal prevalence on faces, terraces and ridges. Elsewhere in the Aorangi Range black beech is limited to dry exposed spurs and ridges within the scrub-hardwood belt. Black beech does not usually grow to altitudes in excess of 1600 feet in the Aorangi Range but occasionally it may be found as pure stands at 1800 feet and scattered trees have been seen at 2600 feet.

2.2.2. Northern and Western South Island

Mountain beech is absent and black beech is uncommon in the vicinity of the Marlborough Sounds. Black beech is usually restricted to rocky littoral sites and the main forests are composed of podocarp species, kamahi, hard beech, red beech and scrub-hardwood species* with some silver beech at higher altitudes. Further inland,

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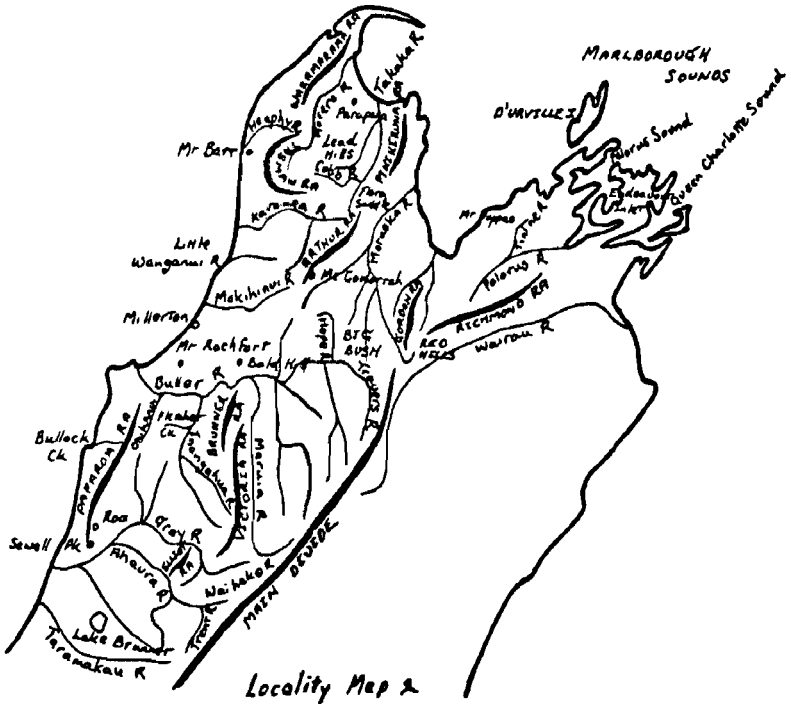
* Scrub-hardwood species are dicotyledonous small tree species which usually attain heights of 15 to 20 feet but are seldom more than 30 feet.

on the alluvial river terraces, in the pockets of forest which have survived land-clearing operations, black beech is an important species. On these sites it is usually found in association with podocarp species but it also grows with hard beech, on some of the drier faces and spurs, up to 1500 feet altitude.

Mountain beech makes its first appearance near Mt Duppa in the headwaters of the Tinline River. Here it occurs on ridges between 2700 feet and 3000 feet, with rata, in a forest zone which is predominantly of silver beech and red beech, with silver beech forming bushline at about 4200 feet. From Mt Duppa down to the vicinity of the Red Hills, near the Wairau River, stands in which mountain beech is associated with red beech, silver beech, Leptospermum species and even mountain cedar, follow the edges of the ultrabasic belt. Mountain beech becomes general near bushline on the south side of the Richmond Range and around the Gordon Range. The mountain beech bushlines in these areas vary between 4300 feet and 4650 feet. Where the bushlines are highest, mountain beech gives way directly to an alpine tussock grassland, but where they are lower there may be an open subalpine scrub belt of Dracophyllum uniflorum and Coprosma pseudocuneata. In the Richmond Range, silver beech joins mountain beech about 200 feet or so below bushline but, towards the west, near the Gordon Range, pure mountain beech may extend down to 3200 feet, which is the level at which red beech first appears. Between 2000 feet and 3000 feet Nothofagus solandri has a very restricted distribution, occurring only as localised pockets on the spurs. In these stands it is intermediate between mountain beech and black beech in leaf characteristics. Below 2000 feet black beech is present on

most of the spurs and river terraces either as pure stands, or codominating with hard beech, silver beech, red beech, podocarps and scrub-hardwood species. On some of the drier sites, especially to the west, black beech may completely dominate the low altitude forest on all sites.



On the rolling, low country on the Moutere gravels along the Motueka River from Big Bush northwards, much of the forest has been cleared or modified by fire but black beech is usually a major component of the stands which have survived. Along the terraces black beech is usually associated with kahikatea, matai, and sometimes with totara, but on the slopes and ridges it occurs with hard beech. Towards the south, red beech and silver beech become increasingly important and are the main tree species in Big Bush. True black

beech is rare in Big Bush but forms intermediate between mountain beech and black beech may form narrow ribbons along streams. The only true mountain beech occurs in the very south where the Moutere gravels reach their maximum altitude. Here, between 2800 feet and 3200 feet, on areas of restricted drainage, mountain beech may form a stunted forest with mountain cedar, Dacrydium biforme and manuka (Leptospermum scoparium).

Black beech occurs throughout the lower alluvial terraces on the eastern side of the north-west Nelson mountain ranges (i.e. the Arthur, Tasman and Wakamarama Ranges) to as far north as the outlet of the Aorere River. It also occurs on the coastline faces of the Pikikiruna Range and on the drier limestone faces within the Aorere catchment but, as far as is known, it is absent from the western side of the Wakamarama Range and the Tasman Mountains. Scattered trees and isolated stands occasionally attain altitudes of 1700 feet but in general black beech is confined to altitudes below 1000 feet. It occurs in association with silver beech, rimu, kahikatea and southern rata (Metrosideros umbellata), and occasionally, towards the coast, with hard beech and northern rata. In the very north of its range it has been seen growing on salty swamps right on the coast together with tanekaha (Phyllocladus trichomanoides), Libocedrus plumosa and various podocarp species.

The forests of the lower and mid-slopes in this North-west Nelson area are usually dominated by red beech, silver beech and occasional podocarps, but hard beech tends to replace red beech as the coastlines are approached. The upper limits of the red beech - silver beech zone extend to 3700 feet altitude south of the Takaka

headwaters but towards the coast in the north they are seldom over 3200 feet altitude, and towards the coast in the west they are even as low as 2500 feet. Silver beech and mountain beech form the upper forests throughout. Mountain beech is more restricted in its distribution than silver beech although either may form the bushline. In the vicinity of Mt Gomorrah, mountain beech forms the bushline but silver beech occurs to within 150 feet of it. At Flora Saddle, silver beech is the bushline species and mountain beech does not appear until 500 feet to 600 feet below the bushline. In the Cobb valley both species reach the bushline and at Parapara Peak, and in the Lead Hills, mountain beech is the bushline species. In the Wakamaramara and Pikikiruna Ranges silver beech again forms the bushline. The level that the bushlines achieve vary, though in a fairly regular fashion. In the south, around Mt Gomorrah, they achieve an altitude of 4550 feet. Further north, at Flora Saddle, they are at 4350 feet. In the Cobb valley they are between 4100 feet and 4300 feet while yet further north around the Lead Hills, Parapara Peak, Heaphy headwaters and the Pikikiruna Range they are between 3950 feet and 4000 feet.

Mountain beech does not occur below 3000 feet in the forests to the south, but in the north, in the vicinity of the Wakamarama Range, it may occur down to 2300 feet. As black beech does not ascend to altitudes above 1700 feet there is always a wedge of at least 1300 feet altitude in the south but narrowing to 600 feet in the north, of red beech - silver beech forest, between the black beech and the mountain beech.

The mountain beech which occurs towards bushline forms a forest

of low species complexity, either dominating alone or with silver beech. At the lower limits of the altitudinal distribution it becomes restricted to ridges and to areas of poor drainage, and on these sites it is usually part of a much more complex community with southern rata, kamahi, Quintinia acutifolia, Dracophyllum traversii and mountain cedar. To the west, in the headwaters of the Heaphy River and around Mt Barr, mountain beech still occupies areas of poor drainage but it also forms stunted forests and scrublands in association with Olearia colensoi, Dacrydium biforme, and sometimes with manuka, on slow-weathering granite surfaces.

The subalpine scrub belt is sparse in North-west Nelson. It is usually composed of scattered, low growing, Dracophyllum uniflorum but is often absent in which case mountain beech and silver beech give way directly to tussock grassland.

Black beech is absent in the western draining catchments of the Karamea, Little Wanganui and Mokihinui Rivers. Mountain beech may form small stands near bushline on some of the sharper inland ridges, or along the sides of the headwater streams but the upper forest is almost exclusively of silver beech. The bushlines, which are formed by silver beech, range from 4300 feet altitude near the headwaters of these rivers, to 3700 feet near the coast.

The forests in the tributaries of the Buller River that drain from the Main Divide, from the Travers River in the north to the Maruia River in the south, are fairly uniform. The bushlines are usually between 4400 feet and 4550 feet though they occasionally ascend to 4700 feet. Above bushline Dracophyllum uniflorum, and

sometimes Hebe species, forms a sparse subalpine scrub belt but the main vegetation is a Chionochloa tussock grassland. Mountain beech is the universal bushline species, with the exception of a few localities in the Maruia headwaters where silver beech forms a lowered bushline at 4000 feet. Silver beech may be present close to bushline in the downstream reaches of these tributaries but towards the headwaters its upper limits are depressed by as much as 600 feet. The highest stands of silver beech tend to be restricted to the faces of more moderate slope and the gullies, and mountain beech becomes limited to the steep faces and spurs. Red beech ascends to between 3400 feet and 3600 feet but, again, towards the headwaters its upper limits tend to be depressed. Close to the main divide mountain beech may form pure stands or codominate with red beech, silver beech or mountain cedar at altitudes below 3000 feet, but elsewhere, below 3000 feet, it is restricted to occasional rocky ridges and bluffs, or along stream channels, and the forest is generally red beech and silver beech. In these isolated, low altitude, ridge and bluff stands mountain beech is often associated with southern rata and kamahi. The mountain beech - mountain cedar forests near the headwaters have a restricted distribution being usually confined to areas where soil drainage is poor or where the parent rock is slow-weathering and close to the surface. Black beech is restricted to small riparian stands along the lower reaches of these tributaries. It is seldom present above 1500 feet but forms, intermediate between black beech and mountain beech, may occasionally occur on spurs up to 2500 feet. It is usually associated with red beech, silver beech, kahikatea and hall's totara, and occasionally on low altitude, downstream spur sites

it may be associated with hard beech.

In the northern Buller tributaries from the Hope River to Bald Hill, and in the Brunner Range, the bushlines are much lower and vary between 3600 feet and 4200 feet. They are generally lowest towards the west and where the drainage is poor or where slow-weathering parent rock is close to the surface. In the west, on the better drained sites the forest is dominated by red beech and silver beech up to 3000 feet. Red beech disappears at this level and between 3000 feet and bushline pure silver beech dominates. Mountain beech only occurs in localised pockets on spurs between 2300 feet and 2900 feet and it is associated with southern rata, kamahi, Quintinia acutifolia, hall's totara, red and silver beech. In the east, the basic pattern of distribution of forest types is similar except that red beech may occur to an altitude of 3500 feet and the pockets of mountain beech are more extensive and usually occupy a higher altitudinal belt, i.e. between 3000 feet and 3700 feet. On the sites where drainage is poor and where the parent rock is erosion-resistant mountain beech may dominate extensive areas even at altitudes as low as 1500 feet and it is usually associated with mountain cedar, Dacrydium biforme, Dacrydium intermedium, southern rata, kamahi, Dracophyllum traversii, silver beech, red beech and manuka. Black beech may occur on the river terraces and ridges up to 1500 feet altitude and occasionally trees with leaf characteristics intermediate between black beech and mountain beech may ascend to 2500 feet. Black beech is usually associated with podocarp species, red beech and silver beech though occasionally it may be found with hard beech. The only known stand of black beech west of Bald Hill and the Brunner Range is

in Fletcher's Creek in the Inangahua valley. Forms intermediate between black beech and mountain beech do occur, however, along the lower Buller River.

To the west of the Bald Hill - Brunner - Victoria - Elliott Range mountain complex is a large area of relatively low lying and often poorly drained land. Here mountain beech is a part of a fairly complex vegetation which varies in composition with the degree of freedom of soil drainage. On the very wettest sites mountain beech is absent and there is a low cover of sedges, manuka and Dracophyllum species. With a slight improvement in drainage mountain beech, Dacrydium biforme, Dacrydium colensoi, mountain cedar, and sometimes Dacrydium intermedium form a low forest. With further improvement Dacrydium biforme and mountain cedar become less abundant and rimu, kamahi, hall's totara and red beech, silver beech and hard beech appear. On the best drained sites mountain beech gives way entirely to the other beech species and to the tall podocarps.

On the hills to the west of this low lying area, the Paparoa Range and the Mt Rochfort mountain system, mountain beech is restricted to bluffs, areas of poor soil drainage and areas where the parent rock is resistant to weathering. Mountain beech appears to be absent from the central Paparoa Range and the forest is made up of red beech, Quintinia acutifolia, kamahi, and podocarp species with silver beech taking over dominance at higher levels and forming the bushline at 3700 feet to 3800 feet. In the central western Paparoa Range, near Bullock Creek, silver beech is restricted to low lying pakihi sites and on the slopes the main forest is one of southern rata, kamahi, Myrsine salicina and rimu. The bushlines in the vicinity of Bullock

Creek are at around 3600 feet and are formed by southern rata, Dacrydium biforme and Olearia colensoi. From north of the headwaters of the Ohikanui catchment in the Paparoa Range through to Millerton, and in the south of the Paparoa Range in the vicinity of Roa and Sewell Peak, mountain beech forms the bushline at between 2650 feet and 3200 feet altitude. These high level stands of mountain beech are seldom more than 10 to 20 feet high and often are dwarfed to less than 3 feet. In them, mountain beech may codominate with a host of other species of which Dacrydium biforme, Dacrydium intermedium, manuka, Olearia colensoi, silver beech, southern rata, Dracophyllum traversii, Dracophyllum townsonii and Quintinia acutifolia are the most important. At lower altitudes red beech, hard beech, hall's totara, rimu and mountain cedar may appear on the sites of better drainage and soil development but on the harsher sites the structure and composition of the stands remains much the same as above. It seems that edaphic factors are here more important than changes in altitude in determining forest composition.

On the western slopes of the mountain ranges which stretch from Bald Hill in the north to the Elliott Range in the south, stands of mountain beech are infrequent and limited to sharp spurs and to sites where the parent rock is close to the surface. From Bald Hill to the southern end of the Victoria Range the forest up to 3700 feet consists of red beech and silver beech but at 3700 feet red beech fades out and silver beech alone forms the forest up to the bushline which is between 3900 feet and 4000 feet. On the western side of the Elliott Range the bushline is only at 3100 feet to 3500 feet and is in most places formed by red beech and silver beech but sometimes

a belt of mountain cedar, Dacrydium biforme and Dracophyllum traversii forest occurs above the beech species. There is a substantial subalpine scrub belt on this side of the Elliott Range which may ascend to 3850 feet in places. This scrub is variously composed of Dacrydium biforme, Dracophyllum uniflorum, Dracophyllum traversii, Dracophyllum longifolium, Olearia colensoi and Phormium colensoi. Below 3100 feet, on the western side of the Bald Hill to Elliott Range mountain complex, southern rata, Quintinia acutifolia and kamahi appear and it is with these species, and sometimes with hall's totara and mountain cedar, that mountain beech is usually associated.

In the upper tributaries of the Grey River, between the Elliott Range and the Main Divide, the upper forest is of mountain beech or silver beech. Towards the Main Divide both species are usually present at, or near, the bushline. At the bushline, which is between 3900 feet and 4200 feet, the beech species give way to a fairly open subalpine scrub belt of Dracophyllum uniflorum, Phormium colensoi, Coprosma pseudocuneata and Chionochloa species. Red beech first appears somewhere between 3000 feet and 3500 feet and at about 2900 feet southern rata, kamahi and Quintinia acutifolia enter stand composition. Mountain beech ceases to be important on the slopes below the upper limits of red beech and occurs only as scattered stands with southern rata, kamahi, Quintinia acutifolia and sometimes mountain cedar. Mountain beech may again assume importance on poorly drained terraces along the valley floors and in these sites it is associated with mountain cedar and Dacrydium biforme. Towards the eastern side of the Elliott Range the bushlines descend to between 3300 feet and 3700 feet and there is a deep subalpine scrub belt of Olearia colensoi,

Olearia lacunosa, Dracophyllum traversii and Dracophyllum uniflorum. Silver beech is usually, but not always, the physiognomic bushline species. Where it is absent the bushline is formed by red beech, mountain cedar, southern rata and Dacrydium biforme. Mountain beech is present on the eastern side of the Elliott Range but is not common.

The Ahaura headwaters of the Grey River have a pattern of forest and subalpine scrub which is more in line with the Taramakau and Hokitika Rivers to the south. There is a dense scrub belt between 3200 feet and 3800 feet which gradually grades into a mountain cedar, Hoheria glabrata, Dracophyllum traversii forest which in its turn grades into a southern rata, kamahi and podocarp forest at the lower altitudes. In the northern tributaries of the Ahaura River, red beech and silver beech stands become superimposed on the basic pattern and may form the bushline. Mountain beech is absent over most of the area but one quite large stand occurs on a western slope, in the lower Trent valley, on an area where the soil mantle is thin. Here mountain beech codominates in a low forest with silver beech, Dacrydium intermedium, southern rata, kamahi and Quintinia acutifolia. Another small stand occurs near the upper limits of forest in the Trent and yet another is known from 3300 feet in the subalpine scrub in the mid Waiheke valley. The Trent stands, and a number of quite large stands in the Otehake branch of the Taramakau River, are the most southerly stands of mountain beech on the West Coast until the vicinity of Paringa is reached. The most southerly known low altitude stand in the northern West Coast is just south of Lake Brunner.

2.2.3. Eastern South Island

In the lower reaches of the Branch tributary of the Wairau River occasional Quintinia acutifolia occur in the low altitude red beech - silver beech - mountain beech forests. This element in forest composition represents a link with the forests on the north bank of the Wairau River. Elsewhere in the southern tributaries and headwaters of the Wairau River, this species is absent and the forests are of low complexity and dominated by mountain beech, red beech and silver beech. The forests, close to the Main Divide, in the upper reaches of the Wairau, Waiau and Hurunui Rivers are generally composed of pure mountain beech from 3800 feet altitude to the bushline which varies between 4100 feet and 4600 feet. Below about 3800 feet silver beech occurs with mountain beech and these two species are joined by red beech at about 3200 feet. From 3000 feet altitude downwards, mountain beech may become a minor forest species on all sites except the steep slopes, rocky outcrops, spurs and young terraces. In the south-west tributaries of the Waiau River and in the Hurunui River, mountain cedar and Dacrydium biforme may co-dominate with mountain and silver beech on bench sites where drainage is poor, between 2500 feet and 3500 feet. Above the bushlines, which are remarkably straight, there may be a low, open, subalpine scrub belt of Coprosma pseudocuneata, Podocarpus nivalis and Dracophyllum uniflorum, but often the mountain beech abuts directly onto grassland. Sometimes in the subalpine scrub belt of the Waiau and Hurunui catchments, Olearia lacunosa, Hoheria glabrata and Dracophyllum traversii may be present but these species are usually restricted to the moister gullies.

Towards the east, first silver beech and then red beech disappears. Their disappearance may be paralleled by an increase in Hall's totara but more often mountain beech becomes the sole tree species and enters into the altitudinal niches left by red beech and silver beech. The forest becomes discontinuous and broken by large areas of tussock and Leptospermum scrub. There is a tendency for the bushlines to become higher and in the upper Branch valley they may reach 5000 feet (M.J. Wraight, 1963), thus forming the highest bushlines in the country. In the Wairau, pockets of mountain beech extend along the Shingly Range to more or less connect with pockets of mountain beech at the northern end of the Kaikoura Ranges but in the Waiau and Hurunui catchments, the eastern limits of these forests are slightly inland from Culverden. The headwaters of the Clarence valley differs from these other three valleys in that it is largely devoid of forest even near the Main Divide.

Red beech and silver beech have a restricted distribution in the Waimakariri headwaters. Some stands of silver beech occur towards the Poulter headwaters and patches of red beech are present, up to an altitude of 3500 feet, in the upper Poulter River and in the vicinity of the Hawdon River. There are also occasional stands of mountain cedar near the Main Divide on bench sites between 2500 feet and 3500 feet but elsewhere in the catchment mountain beech alone dominates the forest. As in the Wairau, Waiau and Hurunui River systems, the bushline in the Waimakariri varies between 4100 feet and 4600 feet. It is around 4100 feet altitude close to the Main Divide but on moving east it increases until in the vicinity of the Waimakariri-Poulter River confluence and the Craigieburn Range,

it may reach 4600 feet. Also, on moving eastwards, the forest becomes discontinuous and on the west faces of the Torlesse and Puketeraki Ranges there are only isolated stands and the vegetation is mainly Dracophyllum scrub and tussock.

Fig. 5 - Forest in the Hurunui catchment. Mountain beech, which is the only tree species above 3800 feet altitude, forms a remarkably straight bushline. Below 3800 feet the forest is composed of red beech, silver beech and mountain beech. (Photo by K. Platt).

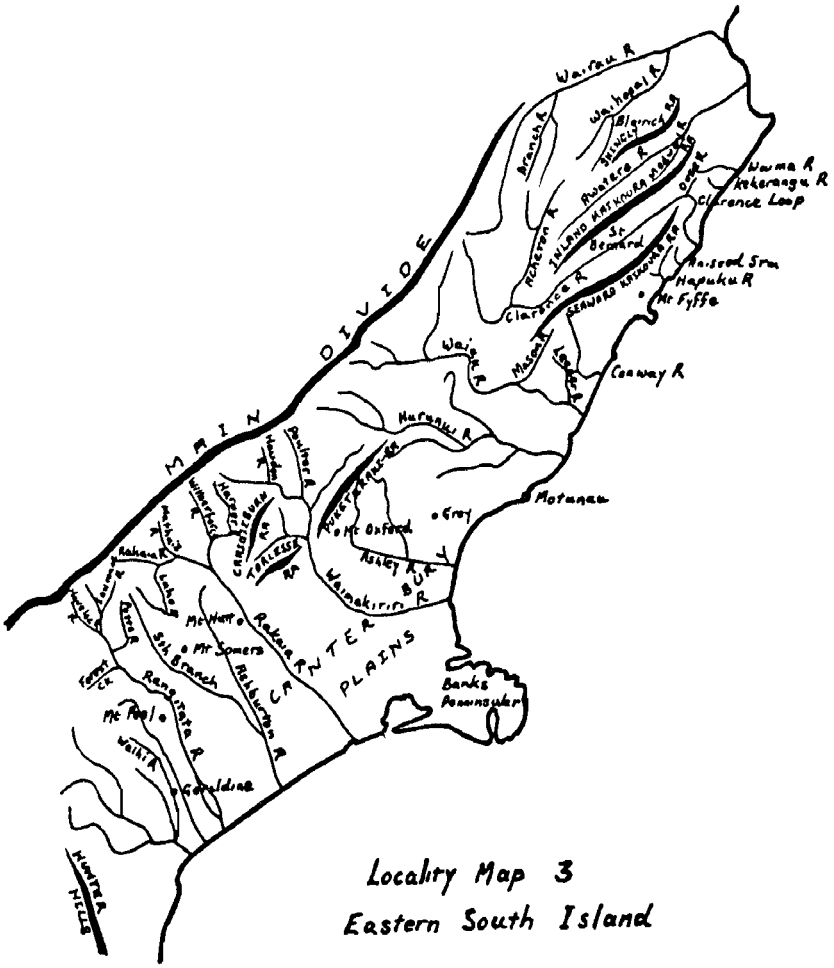
In the Harper branch of the Rakaia catchment, mountain beech alone forms the forests. Red beech, silver beech and mountain cedar are entirely absent and even hall's totara, a species which is usually an element of the forests to the north and south, has a very limited occurrence (only three trees are known).

All the beech species are absent in the upper half of the Wilberforce and Mathias tributaries of the Rakaia River and the

forest is a mosaic of types dominated by hall's totara, Phyllocladus alpinus, mountain cedar, broadleaf (Griselinia littoralis), Dracophyllum traversii and Hoheria, and in at least one tributary, by southern rata and kamahi. The bushline is between 2700 feet and 3000 feet and there is a subalpine scrub of Dracophyllum uniflorum, Dracophyllum longifolium, Podocarpus nivalis and Phormium colensoi. In the lower reaches of these two rivers the forests are mainly restricted to the catchments of the tributary streams. Elsewhere the vegetation is composed of tussock and low scrub. Mountain beech is the main tree species but, up to 3000 feet altitude, there are scattered old trees of hall's totara and occasional mountain cedar associated with the mountain beech. Silver beech is absent and there is only one, unconfirmed, report (J.T. Holloway, pers. comm.) of a single tree of red beech. It is difficult to envisage what the upper limits of mountain beech were in these catchments as so much of the forest has been subjected to repeated burning. However, in one area, in the lower Wilberforce valley, mountain beech does form an apparently natural bushline at 4300 feet altitude before giving way to a low subalpine scrub of Phyllocladus alpinus and Podocarpus nivalis.

In the main Rakaia catchment there are scattered stands of mountain beech from near the confluence of the Rakaia and Wilberforce Rivers to a short distance upstream of the Lake River tributary. Upstream from this point the forests are again of hall's totara, broadleaf and mountain cedar. The islands of forest remaining in the Lake River catchment are limited to between 2000 feet and 3000

feet in the side creeks of the lower 6 to 8 miles of the catchment. These stands are dominated by mountain beech but, in contrast with the rest of the Rakaia catchment, silver beech is also present.



Locality Map 3
Eastern South Island

There are only isolated islands of forest in the Rangitata catchment. Towards the headwaters these are composed of Phyllocladus alpinus, hall's totara, broadleaf and Hoheria but downstream mountain beech is the main, and usually the only, tree species. Silver beech and red beech are absent, but there are specimens of both species in the Armstrong herbarium of the Canterbury Museum labelled as having been collected in the Upper Rangitata River in 1869. Mountain beech occurs between the mid Lawrence and the Potts

tributaries on the true left, and between the mid Havelock River and Forest Creek on the true right of the Rangitata River, but most of the stands of this species are confined to the tributary creeks. The upper altitudinal limits of mountain beech are usually depressed but in two areas, one in the lower Lawrence catchment and the other in Forest Creek, mountain beech reaches what appears to be a natural bushline. In both areas this is at about 3800 feet. Apart from occasional stands of Hoheria lyallii and other small scrub-hardwood species bordering some of the tributaries, there is no forest downstream from Forest Creek until the neighbourhood of Mt Peel is reached. The forests at the higher altitudes around Mt Peel are dominated by hall's totara and there are occasional stands of mountain cedar. At the lower levels matai (Podocarpus spicatus), true totara (Podocarpus totara) and kahikatea occur over a dense scrub-hardwood tier of mahoe, broadleaf, lancewood (Pseudopanax crassifolium), Pittosporum tenuifolium, and Pseudopanax arboreum. Mountain beech has been found on two sites only, one a spur facing the east and the other a broken ridge and bluff to the north. These stands both occur between 1500 feet and 2000 feet.

To the south of Mt Peel, matai, true totara and scrub-hardwood stands continue along the eastern foothills behind Geraldine and along the eastern side of the Hunter Hills but in these stands mountain beech has only been found in two places. One small stand of mountain beech occurs about six miles to the south of Mt Peel, and, near the headwaters of the Waihi River there is another small stand at about 1200 feet altitude. In both there is a strong representation of scrub-hardwood species in the understorey.

From the Rangitata River north to Mt Grey, the forests along the foothills bordering the Canterbury Plains are dominated by Nothofagus solandri. At lower altitudes the Nothofagus solandri has strong affinities with black beech but higher up it becomes unmistakably mountain beech. Silver beech and red beech both occur but are subordinate to mountain beech and both have very localised distributions. Silver beech occurs only to the south and west of Mt Somers and red beech occurs in the proximity of Mt Grey. C. Burrows (pers. comm.) states that red beech is also present near Oxford. Kahikatea, and less frequently pokaka (Elaeocarpus hookerianus), may be associated with Nothofagus solandri at low altitudes and at the southern end of the Puketeraki Range there are some rimu and matai. Occasional small stands of rata occur near Mt Somers and occasional trees of kamahi occur near Mt Grey but over most of the region mountain beech, and forms intermediate between mountain beech and black beech, are the only large tree species. It is only rarely that mountain beech ascends to a natural bushline. Where it does, around Mt Oxford and Mt Somers, the upper limits are usually between 4000 feet and 4150 feet. The subalpine scrub above the bushline is variously composed of Dracophyllum uniflorum, Podocarpus nivalis, Phyllocladus alpinus, Coprosma pseudocuneata and Hebe species.

A few small stands of mountain beech occur on Banks Peninsula. Most of the forests here have been destroyed by fire and those which remain are usually dominated by hall's totara, matai and scrub-hardwood species. The stands of mountain beech are restricted to the extreme south-east corner and occur at around 2000 feet with red

beech, hall's totara and rare mountain cedar.

Further north along the coast near Motunau there are again a few stands of mountain beech but it is not until north of the Conway River, in the Seaward Kaikoura Range, that Nothofagus solandri forest, or in fact any forest, becomes extensive on the coastal ranges.

Forest is more or less continuous on the eastern side of the Seaward Kaikoura Range. Here there is a complex mosaic of associations related to the unstable geological nature of the country and to the long history of burning both in pre-European and in European times. The extent of this burning is evidenced by the consistent presence of charcoal underlying many, of not most, of the present forest stands. Hall's totara is the main species at higher altitudes and forms a bushline at around 3300 feet. It is replaced below 2000 feet by matai - hall's totara forest, pure matai forest, and, especially to the north of Mt Fyffe, by mixed podocarp forest with true totara, kahikatea, rimu, matai and miro. Superimposed on this pattern of forest types are the scrub-hardwood and Leptospermum communities. Fuchsia (Fuchsia excorticata)-wineberry may occupy the steep, rapidly downcutting gullies. Mixed Pseudopanax arboreum - broadleaf - mahoe scrub-hardwood may occupy moist, sheltered faces and below 700 feet, near the coast, coastal scrub-hardwood, with ngaio (Myoporum laetum) and titoki (Alectryon excelsum), is the main forest type. Leptospermum forest and scrub in important on drier sites where there has been fairly recent burning or where farmlands have been allowed to revert to scrub. Red beech is an important forest species below 1000 feet

on sheltered, moist river terraces and gently sloping gullies which have escaped recent fire, south of Mt Fyffe, but it is rare between Mt Fyffe and the lower reaches of the Clarence River.

Nothofagus solandri is present throughout the eastern side of the Seaward Kaikoura Range. It occurs with all the plant communities mentioned above though usually as a scattered emergent tree and seldom forming a pure stand. Typical mountain beech is not common. It forms isolated stands with hall's totara, miro, kanuka, and red beech and occasionally with mountain cedar, on dry spurs between 2500 feet and 2800 feet on Mt Fyffe, and in some of the southern tributaries of the lower Clarence River it may form a bushline at around 4100 feet altitude. It also occurs on the mid slopes in the north branch of the Hapuku River but here it gives way at its upper limits to hall's totara. Elsewhere Nothofagus solandri has some of the leaf characteristics of black beech and is limited in distribution to between sea level and 2500 feet. Close to sea level it is very close to black beech in leaf shape. An interesting association between Nothofagus solandri, tawa and mixed podocarp species occurs in the Aniseed stream and has been described in detail by P. Wardle (1961).

With the exception of an area of scenic reserve located near the headwaters of the Waima and Kekerangu Rivers, forest cover north of the Clarence River is scattered and the Waima catchment more or less delineates the northern boundary of true forest until the north bank of the Wairau River is reached. The forest in the reserve is dominated by red beech, a form of Nothofagus solandri intermediate between black beech and mountain beech, and hall's totara. Between

this reserve and the Clarence Loop, the vegetation is largely Leptospermum scrub though there are patches of ngaio-dominated scrub-hardwood close to the coast, and in the Ouse tributary of the Clarence River there are scattered stands of mountain beech, red beech and hall's totara.

There is very little forest in the Clarence catchment upstream from the Clarence Loop. In the very north of the inland faces of the Seaward Kaikoura Range there are occasional small stands of hall's totara and mountain beech but elsewhere there is Leptospermum scrub, grassland, and rare islands of Hoheria lyallii. Even Leptospermum is rare over most of the inland side of the Seaward Kaikoura Range. On the north-west side of the Clarence River, against the Inland Kaikoura Range, however, mountain beech and hall's totara occur in most of the sheltered gullies to as far south as St. Bernard Peak.

There is much the same pattern of forest distribution in the Awatere catchment. The only known patch of forest on the south-east side of the river is in the headwaters of the Medway River (J. Gibson, pers. comm.). This is composed of mountain beech, but on the north-west side of the river there are small patches of mountain beech in many of the tributaries from Blairich Peak to the headwaters.

Forest is absent from the Clarence catchment between St. Bernard Peak and the Acheron River. In the headwaters of the Acheron River and its tributaries, and in the Clarence for a short distance upstream from the Acheron-Clarence confluence, occasional small stands of mountain beech occur in the gullies but the main vegetation is tussock grassland. To the south, in the headwaters of the Mason and Leader Rivers, there are again small patches of mountain beech and

also red beech and hall's totara but the areas which have not been converted to farmland are generally Leptospermum scrub or mixed scrub-hardwood forest.

Fire has had an important influence on forest distribution on the eastern side of the South Island and many areas which are now scrubland or grassland show charcoal evidence of a former forest cover (see Molloy et. al., 1963). The full extent of the influence of fire on the present forest distribution is not known, and there is often no evidence to suggest that forests would now be capable of maintaining themselves on sites where charcoal suggests that they once occurred. For this reason the influence of fire on the present geographic distribution of Nothofagus solandri is considered to be beyond the scope of this thesis.

2.2.4. Southern South Island

South of the Rangitata River all the beech species are absent until the west bank of the Tasman River is reached. Here mountain beech and silver beech make their first appearance. The scattered pockets of forest which occur in the Godley and Macaulay Rivers and on the east bank of the Tasman River as well as in the headwaters of the Tasman River on the west bank, are composed of hall's totara, Phyllocladus alpinus, broadleaf and Hoheria. The beech forests lower down the Tasman River are generally confined to the tributary creeks between the Hermitage and Lake Pukaki. The stands furthest upstream, both in the side creeks and in the headwaters, are of silver beech, but in all cases mountain beech takes over dominance lower down.

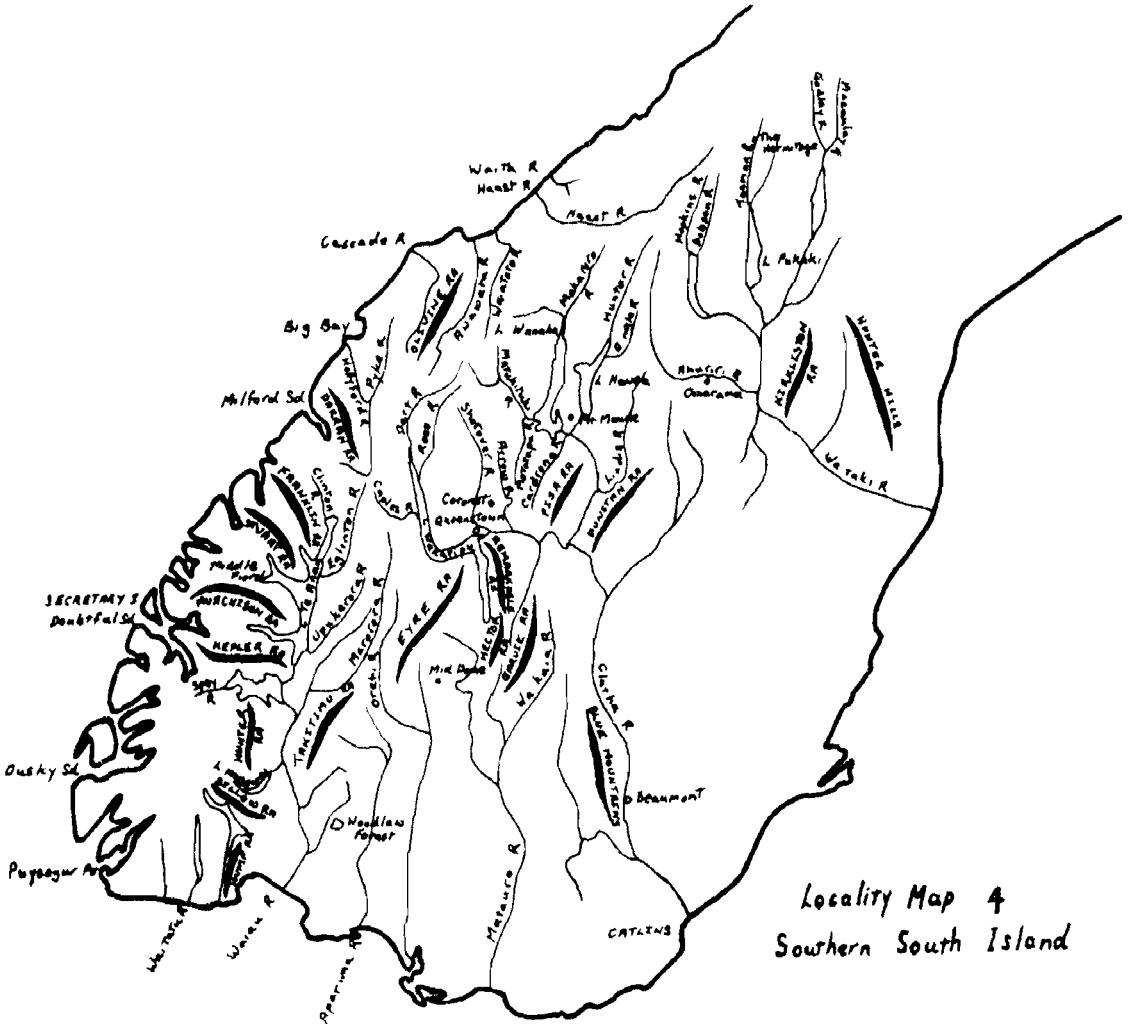
From the Tasman River south, throughout the headwaters of the Waitaki and Clutha catchments, Nothofagus species dominate the forests and in general silver beech in the main species close to the Main Divide but gives way to mountain beech downstream. The extent of the silver beech forest increases from north to south. Thus in the Dobson and Hopkins catchments silver beech is the main species in the upper few miles of forest only, while in the Hunter catchment silver beech dominates the forests in the upper half of the valley and occurs with mountain beech throughout the remainder of the catchment. Still further south in the Makarora catchment, at the head of Lake Wanaka, there are only occasional mountain beech (A. Mark, pers. comm.), and silver beech is the dominant species throughout. In the Matukituki, Rees and Dart valleys, red beech, which first makes its appearance as a small stand at the head of Lake Hawea (this is with the exception of one unconfirmed record from the Waitaki headwaters), codominates with silver beech on the lower slopes up to 2500 feet or even 3000 feet altitude, but gives way to silver beech and mountain beech with further gain in altitude. Again mountain beech becomes progressively subordinate to silver beech towards the headwaters and in the Matukituki valley, and probably also in the Dart and Rees valleys, mountain beech is absent from the stands furthest upstream.

In the Ahuriri and Dingle catchments where the headwaters are some distance from the Main Divide, silver beech is only a minor component of the forests. In the Dingle catchment there are only a few isolated trees of silver beech near the up-valley forest limits and the forest is otherwise entirely composed of mountain beech.

The upper altitudinal limits of forest show a marked variation

between catchments. In the Dobson valley the bushlines are at their lowest, around 3600 feet, and in the Hopkins, which is the next catchment going southwards, they are nearly always around 3950 feet. In the Ahuriri and upper Dingle valleys they are between 3300 feet and 3900 feet and in the lower Dingle they may reach 4100 feet. The bushlines in the Hunter valley are between 3700 feet and 4000 feet and in the Matukituki valley are between 3700 feet and 3800 except near the valley head where they drop to almost 3000 feet. In the Dart and Rees valleys they are again low near the headwaters but rise to 4000 feet down-valley. The only regular trend in the altitude that the bushlines achieve is that they tend to increase away from the Main Divide. Silver beech forms most of the upper valley bushlines even after mountain beech appears. Mountain beech is usually limited to the valley floors, spurs, and alongside the steep gradient tributaries near the headwaters. Further downstream it gradually eases its way up through the silver beech forest to ultimately take over the bushline and silver beech becomes restricted to the lower and middle slopes. From the Dingle River northwards, in these downstream reaches, silver beech then disappears out entirely, giving way to pure mountain beech forest.

Above bushline the subalpine scrub is fairly uniform in composition and the physiognomic species are usually Podocarpus nivalis, Phyllocladus alpinus, Coprosma pseudocuneata, Dracophyllum uniflorum and Dracophyllum longifolium. This belt of subalpine scrub is narrow and open in the north but to the south becomes wider and denser and Olearia colensoi and Olearia moschata may become locally important.



Mountain cedar is represented in the mountain beech forest on benched sites at around 2000 feet near the junction of the east and west branches of the Matukituki River. Holloway (1954) records the possible occurrence of another such stand in the Hunter valley. Southern rata and kamahi occur with mountain beech on occasional bluffs and rocky ridges in the Matukituki and Hunter catchments and occasional kamahi are also present in the Dart and Rees valleys and may form an understorey to the mountain beech forests. In at least one area in the Hunter valley, on a smooth rocky spur with a thin soil mantle, Dacrydium biforme codominates a low mountain beech,

silver beech forest in which hall's totara and manuka are also important species.

The forests in the Caples valley are again composed of silver beech in the headwaters and mountain beech towards the lower reaches. In the Eglinton and Upukeroro valleys further south mountain beech is rare and occurs only in scattered low altitude stands on the valley floors between 1100 feet and 1200 feet except towards the eastern shores of Lake Te Anau where it tends to become more prevalent. Where it occurs it is associated with red beech and silver beech and occasional rimu, miro and hall's totara. Elsewhere the forests are entirely of red beech and silver beech, but from the Mararoa headwaters southwards, in the Oreti headwaters upstream from Mid Dome, and in the upper Mataura valley, red beech has a restricted distribution. The forests throughout this southern section of the Eyre mountains are discontinuous but they have a remarkably uniform composition. Mountain beech and silver beech codominate throughout up to the bushline which is between 3500 feet and 3700 feet. Except in the furthest upstream forest stands, red beech may join the mountain beech and silver beech below 3800 feet on the gentler slopes and moister sites.

Isolated pockets of mountain beech - silver beech forest, with occasional red beech, also occur in some of the valleys which lead into the southern crook of Lake Wakatipu from the west. Further to the east, in the upper Waikaia valley, the forest is again of silver beech, red beech and mountain beech. All three species are present below 2300 feet, but between 2300 feet and the bushline which is at 3000 feet altitude, silver beech alone is present.

To the south-east of the Waikaia River, in the Blue Mountains Range, silver beech dominates the higher altitude forest and red beech and podocarp species are important lower down, but on old terraces alongside the Clutha River from Beaumont downstream for about ten miles are stands which include some mountain beech. These stands, which are at about 600 feet altitude above sea level represent the furthest south-east distribution of mountain beech in the country.

To the north, the Hector and Remarkable Ranges form the eastern limits of mountain beech and in fact of most tree species until the coast is approached. The occasional pockets of forest which remain on the western flanks of these ranges are confined, by and large, to the sheltered gully sites. In them, mountain beech and silver beech are the main tree species but there is usually some red beech and hall's totara. Still further to the north, there are scattered patches of forest in the gullies and along the slopes facing Lake Wakatipu upstream from Queenstown, and in the Shotover and Arrow catchments upstream from Coronet Peak. The stands alongside Lake Wakatipu are composed of mountain beech, red beech and hall's totara but in the Shotover valley pure red beech and hall's totara are absent though hybrids of both occur (P. Wardle, 1966). Most of the Shotover stands are in gorges, narrow gullies and on lake or river banks though isolated trees and groves of trees are found even on exposed rocky spurs. Mountain beech is the only tree species over most of the area but in the lower Shotover valley silver beech occur, as small, widely-scattered stands within the mountain beech. The upper limit of mountain beech in the Shotover valley is generally around 3500 feet, though it does attain 4000 feet altitude in places.

There is a scant subalpine scrub belt in places and in it the main species are Dracophyllum uniflorum and Podocarpus nivalis.

In the Arrow valley the largest areas of forest are near Coronet Peak. These are again predominantly of mountain beech, but silver beech, hall's totara and red beech are all present. Elsewhere in the Arrow catchment there are only small stands of forest or isolated trees in the gullies.

Further north, the eastern limit of mountain beech is marked by small stands in the lower Motatapu tributary of the Matukituki River and in the tributaries on the western side of the middle and lower Cardrona valley. A. Mark (pers. comm.) has found four small stands of silver beech in the Cardrona valley and two of these contain some mountain beech. There are occasional trees of silver beech, but no mountain beech at the north end of the Pisa Range. On the eastern slopes of Mt Maude facing the southern end of Lake Hawea, there are a few stands of mountain beech in sheltered gullies. At least one of these stands contains some silver beech and hall's totara. There are stands of pure mountain beech on the opposite side of the southern end of Lake Hawea and near the head of the Lindis River and there are unconfirmed reports of mountain beech south of Omarama. To the east of these mountain beech and silver beech outliers, the only tree species is hall's totara which occurs in the Pisa Range, in the Lindis area and in the Hunter Hills Range. Logs of hall's totara have been found in the Kirkliston Range though no living trees remain. Mountain beech is completely absent from the Hunter Hills and the other coastal ranges and forests in the south-

east of the South Island until the Waiau River is approached. Even on pakihi sites in the Catlins district where there is Dacrydium intermedium, mountain cedar and stunted rimu, there is no mountain beech.

The first mountain beech in the far south appears in the Woodlaw Forest where there are one or two trees of the species scattered amongst what is a predominantly silver beech forest (J.T. Holloway, pers. comm.). Mountain beech also occurs in the headwaters of the Aparima River, on the eastern flank of the Takitimu Range, on the gentler slopes and terraces where soil drainage is impeded and on some spurs below 2500 feet. Nowhere does it approach the bushline which is entirely of silver beech and occurs at around 3200 feet altitude.

The eastern Takitimu and Woodlaw distributions of mountain beech are isolated ones and the species is absent from the remainder of the Aparima catchment and to the west until the proximity of the Waiau River is reached. The Waiau River becomes the eastern limit of distribution north of Woodlaw Forest and the Orauea tributary of the Waiau River becomes the eastern limit of distribution south of Woodlaw Forest (J.T. Holloway, pers. comm.).

Throughout the low lying hill country and terraces to the south of Lake Monowai and extending west from the Waiau River along the coast past the Waitutu River and possibly as far as Puysegur Point, the forests are predominantly of silver beech and podocarp species, mainly rimu. Mountain beech is present throughout, though overall it is less important than either silver beech or rimu. It occurs on the coastal escarpment often as pure stands with windroofed

canopies down to 50 feet or so above sea level where frequently it is under the direct influence of sea spray. Further inland the pure stands of mountain beech grade first into mountain beech - silver beech, then into mountain beech - silver beech - podocarp and finally into silver beech - podocarp and pure podocarp stands. This may all take

Fig. 6 - Mountain beech on the coastal escarpments west of the Southern Waiau River. Mountain beech on these sites often occurs as pure stands with windroofed canopies down to 50 feet or so above sea level and is frequently under the direct influence of sea spray.

place within a few chains. With the exception of the coastal escarpments, mountain beech is rare close to the coast but further inland it becomes progressively more important although nowhere does it become more important than silver beech and its distribution tends

to be limited to the proximity of streams, areas of fairly poor soil drainage, old slips and fire scars and to the drier spurs. Pure stands are rare and the species is nearly always associated with silver beech. Rimu, kahikatea and miro may also be present, and on areas of poor drainage on the terraces west of the Wairauahiri River, mountain beech may be associated with Dacrydium biforme, Dacrydium intermedium and manuka (J.T. Holloway, pers. comm.). Association between red beech and mountain beech is rare as red beech is known only from three small stands just south of Lake Monowai (J.T. Holloway, 1954).

The mountain beech in this area is somewhat atypical for the species, both in the large size of the adult leaf, in the form and size of the adult tree, and also in the form and leaf shape of the juvenile plant. The adult leaves, though much larger in size than is usual for mountain beech are definitely typical of mountain beech in shape. The juvenile leaves on the other hand often tend to be orbicular in shape and the branches of the juvenile plant often tend to be intertwined, both features being characteristic of black beech rather than mountain beech.

In the mountain ranges of eastern Fiordland, silver beech is the major tree species but mountain beech is usually present and increases in importance from south to north until in the vicinity of the eastern Murchison mountains it is probably as important as silver beech in the forests at higher altitudes. The bushlines which are at around 2900 feet altitude in the Hump Range are generally of silver beech and mountain beech is absent from the upper 300 feet to 500 feet of forest except on some specialised sites. J.T. Holloway (1954)

has stated that on the western side of the Hump Range there are two main rock types - the basal coal measure sandstones and the coarse conglomerates; and, on the upper slopes silver beech is the dominant or the only species on the conglomerates with mountain beech dominant, or the only species on the sandstones. On the poorer sites mountain beech forms a low forest with southern rata and Dacrydium biforme but where there is a moderate soil development mountain beech usually occurs with silver beech. Further north on the Billow and Hunter Ranges and at the eastern end of the Kepler Range, the bushline is between 3200 feet and 3300 feet and although silver beech is invariably a dominant species at bushline, mountain beech is frequently also present. The composition of the upper forest is less complex than in the Hump Range and there is a less pronounced subalpine scrub belt. In the Hump Range the subalpine scrub is composed of Dracophyllum uniflorum, Phyllocladus alpinus, Coprosma pseudocuneata, Dracophyllum menziesii and Olearia colensoi but here it is usually of Coprosma pseudocuneata, Dracophyllum longifolium and Dracophyllum uniflorum only and sometimes the forest gives way directly to Chionochloa species. The forests of the lower slopes are still composed of silver beech and mountain beech but below 1700 feet altitude hall's totara appears and below 1400 feet there may be some rimu, miro, kahikatea, and, in the eastern Kepler Range, red beech.

In the eastern Murchison Range mountain beech is dominant in the upper forests (C.J. Burrows, pers. comm.). Still further north, in the eastern Stuart, Franklin and Darran Ranges, there is a rapid change in the distribution of the beech species and mountain beech becomes restricted to occasional stands on the lower terraces. Silver

beech again is the only large tree in the upper forest belts and it forms the bushline at between 3200 and 3300 feet.

On moving west through Fiordland from the eastern ranges to the central ranges, the same types of trend in the distribution of forest types and in forest composition occurs, as has been described for the eastern ranges between the Murchison Range in the north and the Hump Range in the south. In the eastern ranges, the bushlines in the Billow Range and further north are between 3200 feet and 3300 feet altitude, while those in the south, on the Hump Range, are only 2900 feet. Likewise there is a tendency for the bushline to be lower in the central ranges than in the eastern ranges. Thus at the head of the Clinton valley the bushline is only 3050 feet and at the head of the middle fiord of Lake Te Anau (Scott, Mark and Sanderson, 1964) and in the Spey valley it is only 3000 feet. There is the same tendency for mountain beech to become restricted to sites where the soil mantle is thin and the parent rock resistant to weathering, to sites where soil drainage is poor, and to landslides. Red beech disappears and silver beech becomes the physiognomic tree species between the valley floor and the bushline. Southern rata and kamahi become more important in the composition of the forest and Olearia colensoi appears as a constituent of the subalpine scrub and bushline forests. Where mountain beech occurs on old landslides it is usually associated with silver beech and often with southern rata, kamahi and hall's totara. On areas of poor drainage and thin soil mantles, though, Dacrydium biforme and manuka are usually codominant with mountain beech.

Further to the west, in the vicinity of the fiords, the country

becomes much steeper, and areas of weakly weathered parent rock and sites of poor drainage, more extensive. Mountain beech, which is an important species on these harsh sites, again tends to increase. Soil drainage and stage of soil development have a very pronounced influence on forest structure and composition and changes in these physical factors may result in a change from a low scrub in which mountain beech is the dominant species to a tall forest in which silver beech dominates and mountain beech is a minor species, or even absent, all within a matter of half a chain or so. Mountain beech can attain altitudes here as high as those reached by silver beech. The upper altitudinal limits of both species are very irregular but even so there is a strong tendency for the extreme upper limits of both to be lower than in central Fiordland. As mentioned previously, the upper limits in central Fiordland are usually at around 3000 feet altitude but here they are seldom more than 2800 feet or 2900 feet, i.e. towards the head of Dusky Sound they are around 2900 feet and towards the heads of Doubtful Sound and Milford Sound they are at 2800 feet. An exception to this general trend is given by P. Wardle (1963) for Secretary Island where he records that both beech species occur at 3200 feet.

Where mountain beech occurs on areas of impeded soil drainage at high altitudes it is usually associated with Dacrydium biforme in a stand which is seldom more than 20 feet high and silver beech is a minor species. Below 2500 feet southern rata, kamahi, and manuka are often also present. If the drainage deteriorates further, the above species tend to be confined to hummocks separated by mats of close growing herbs and sedges, or, on the other hand, the beech

species, southern rata, and kamahi may grade out leaving manuka and Dacrydium biforme. With improvement in drainage, the height of the stand increases and silver beech replaces mountain beech. Below 2000 feet hall's totara may occur in these poorly drained sites and below 1300 feet rimu also may be present, and occasionally, close to sea level, there may be some kahikatea.

Where rock is close to the surface, again mountain beech and Dacrydium biforme codominate. Manuka and southern rata are usually present below 2500 feet and silver beech is more frequent here than on the poorly drained sites. These stands are usually less than 10 feet high, and sometimes, where soil development is restricted to rock crevices, may be no more than 1 foot 6 inches high. Below about 1900 feet altitude, especially where there is a thin peat developed

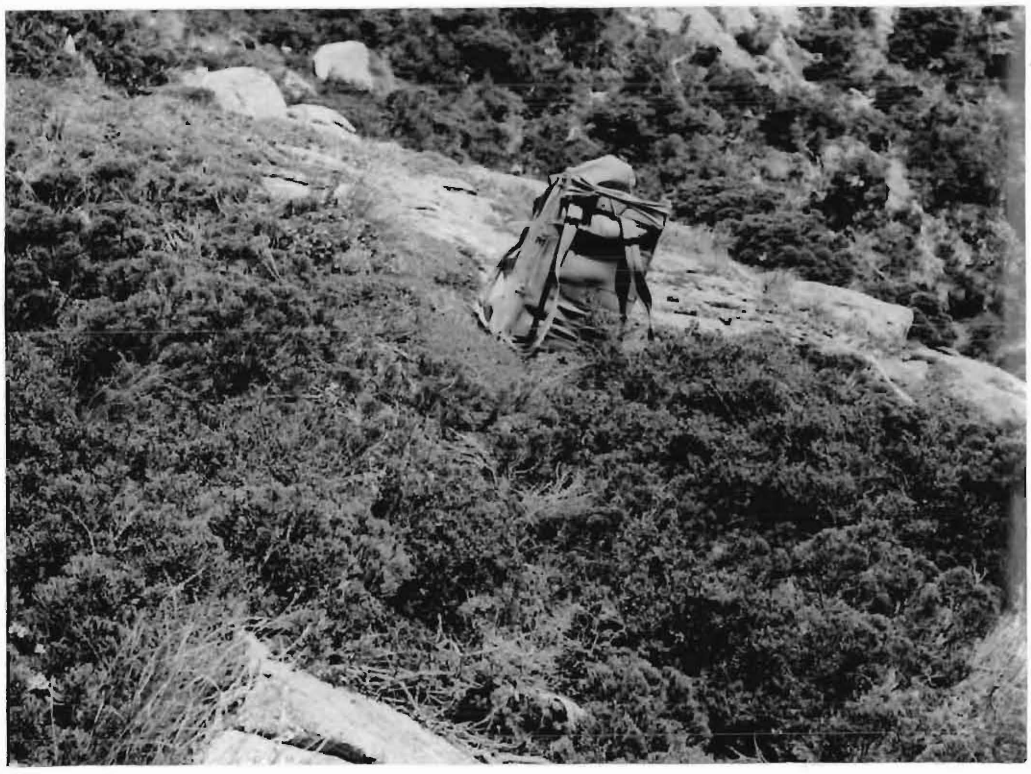


Fig. 7 - Lake Mike, near the head of Dusky Sound. Where soil development is restricted to rock crevices, mountain beech may form stands which are no more than 1 ft. 6 in. high.

over the parent rock, Dacrydium intermedium is associated, but otherwise there is little change in composition. But, towards sea level, on rock spurs which have been overridden by ice, kamahi, hall's totara, rimu, and miro tend to replace Dacrydium biforme and manuka. Mountain beech, southern rata and Dacrydium intermedium, however, still remain important species.

On the fiord walls, where the slopes are excessively steep, the development of a woody vegetation eventually results in the formation of a landslide. Once the vegetation becomes too heavy to be supported by the steep slopes it sheers off the rock faces and a new surface is exposed. Mountain beech is usually a part of the seral vegetation, but its occurrence is sporadic and silver beech is the dominant tree species. If the site remains stable for long, silver beech gradually excludes the mountain beech but if slumping recurs a niche for mountain beech is preserved. In the fiords, mountain beech is often found growing right at sea level with its foliage overhanging salt water.

Towards the Hollyford River, in the north, the part played by mountain beech in forest and scrub composition becomes less pronounced. Mountain beech is absent from quite large stretches of country, especially towards the headwaters of the westward flowing rivers and streams. Silver beech becomes the only important tree species though stands of red beech do occur at the head of Milford Sound and from the mid Hollyford valley northwards.

Further north, between the Arawata River and the sea, mountain beech again becomes quite an important species. The forests of this area are best described by summarising notes written by J.T.

Holloway and supplementing it for certain areas by field notes taken by J. Holloway and myself. Silver beech is the physiognomic species up to the bushline which is generally around 3300 feet altitude. Below 2000 feet red beech may codominate and at lower altitudes, somewhere below 1500 feet, the podocarp species, mainly rimu but also kahikatea, miro, matai and totara supplement the forest composition, and locally, on the slopes, southern rata and kamahi may assume dominance. Mountain beech again tends to be restricted to areas of poor drainage and infertile and slow-weathering parent rocks. It is also a strong component of the coastal scrub.

Where the ground is wet and boggy, mountain beech tends to be associated with manuka, Dacrydium bidwillii, Dacrydium biforme and Dacrydium colensoi. In the worst drained areas, mountain beech is absent and the bog vegetation consists of stunted manuka, Dacrydium bidwillii and Dracophyllum species. On the other hand, with improved drainage, stunted southern rata, mountain cedar, and Dacrydium intermedium become important. Large areas of scrub of this nature occur on the plateaux to the north of the Cascade River and at the north side of Big Bay, and probably also on the plateau remnants on either side of the Hollyford outlet. In the vicinity of the Cascade valley this type extends from a few hundred feet above sea level to 1900 feet altitude. With further improvement of drainage on these sites, silver beech and mountain beech may codominate with rimu, southern rata, kamahi, and Dacrydium intermedium at the lower altitudes but as drainage becomes better still, Dacrydium intermedium and mountain beech give way completely to silver beech, rimu, southern rata and kamahi. Except where the high cliffs of the Cascade Plateau

fall to the sea, there is generally a wide belt of coastal scrub along the coast between the Arawata River and Hollyford River mouths. Typically this is composed of gnarled, windswept southern rata and kamahi but frequently mountain beech, silver beech, manuka and stunted rimu are also present.

The eastern slopes above the Pyke branch of the Hollyford River are frequently steep and have very little soil development and here mountain beech usually co-dominates, in a low forest which may be less than 4 ft high, with Dacrydium biforme, southern rata, silver beech and sometimes Dacrydium intermedium. In some places the vegetation may be reduced to stunted manuka and southern rata less than 1 foot high. It is only as a component of this type of forest on slow weathering and infertile parent rock that mountain beech ever reaches the bushline in this area.

Large areas of infertile ultrabasic rock occur along the alpine fault to the east of the Pyke headwaters and the Cascade River. In general these areas are largely barren of forest and scrub but, according to J.T. Holloway, where schist screes from the Olivine Range descend across them, a poor scrub of manuka, mountain beech, southern rata and various scrub composites occurs and scattered rimu may also be present. Within the mineral belt, silver beech is generally restricted to valley floor stands where the alluvium contains materials of schist origin.

Mountain beech has a very restricted distribution on the west coast north of the Arawata River, at least until the Taramakau River is reached. It is only known to occur near the head of the Waiatoto River (A. Mark, pers. comm.) and in the vicinity of the Waita River.

The Waita mountain beech is nearly always associated with silver beech, rimu, and kamahi. The forests north of the Arawata River are composed, by and large, of silver beech towards bushline, of silver beech, southern rata, kamahi and rimu on the lower slopes, and of various combinations of miro, hall's totara, kahikatea, Dacrydium intermedium, Dacrydium biforme, Dacrydium bidwillii, Dacrydium colensoi, mountain cedar, manuka, and silver beech towards the coast. Silver beech grades out north of the Haast River and the forests of the higher slopes then become composed of hall's totara, mountain cedar, southern rata and kamahi.

All the beech species are absent from Stewart Island and the forest is largely composed of podocarp species, southern rata and kamahi. The altitude that the bushline attains varies considerably and above bushline there is a dense scrub belt in which Olearia colensoi is an important species.

2.3. SUMMARY AND CONCLUSIONS

The most extensive forests of Nothofagus solandri are on the east side of the Main Divide in the South Island. Here pure stands of the species may abut onto areas of Leptospermum scrub or tussock grassland. These stands, which represent some of the driest forests in the country, may in some cases, such as in the vicinity of the southern end of Lake Hawea, occur where the annual rainfall is less than 40 inches per annum* but more often the 40 inch isohyet more or

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* When generalised statements are made referring to rainfall the source of information is the N.Z. Meteorological Dept's. 4 mile to the inch unofficial rainfall map of New Zealand.

less delineates the present boundary of the species.

The highest bushlines in the country are in the Branch and Leatham tributaries of the Wairau River, and on the southern and western sides of Mt Ruapehu. In the vicinity of Mt Ruapehu, forest reaches 4950 feet altitude while in the Branch and Leatham it reaches altitudes in excess of 5000 feet. In both cases Nothofagus solandri is the sole tree species at the bushline.

Under the conditions of high rainfall such as on the western side of the Main Divide, Nothofagus solandri is usually absent in the forests at low altitudes from all but the harshest and youngest sites. It is usually only present where soil drainage is impeded, where the parent rock is resistant to weathering and the soil mantle is consequently thin or on spurs, terrace rims or coastal escarpments, or as a component of seral vegetation, but on any of these sites it may dominate the vegetation.

It seems that Nothofagus solandri is a species with a wider range of tolerance for conditions of low rainfall, high altitude, poor soil development and poor soil drainage than most New Zealand tree species, but that it is a species which has a low ability to compete with other trees and shrubs where conditions are improved and the site becomes more generally suitable for forest growth. If we hypothesize that Nothofagus solandri is such a species with a wide range of tolerance for harsh conditions but with a poor competitive ability then many of the apparent anomalies in its distribution fit into an explicable pattern. For instance it explains why, in the Huiarau and Raukumara Ranges in the North Island, the species is restricted at high altitudes to occasional knobs and spurs near bushline

but at the same time may occur on spurs on the foothills of the ranges. The rainfall is almost certainly much lower on the foothills than elsewhere and whereas the presence of the species at these lower altitudes, on the spur sites, may result from the tolerance of Nothofagus solandri for low moisture conditions, the presence of the species near the bushline may result from its tolerance for the harsher temperature conditions prevailing at high altitudes. Its absence elsewhere would result from the inability of the species to compete with other tree and shrub species under the conditions of improved rainfall and lower altitude. On moving south-west towards the central North Island, rainfall decreases and Nothofagus solandri becomes more general at higher altitudes and descends progressively lower.

If Nothofagus solandri is a species with high tolerance for harsh sites but low competitive ability then this could explain why, on the eastern side of the South Island, pure Nothofagus solandri forest tends to give way first to red beech at low altitudes, and then to silver beech at high altitudes as the Main Divide is approached. This could be related to a low ability in Nothofagus solandri to compete with red beech at low altitudes and with silver beech at higher altitudes under the conditions of higher rainfall prevailing close to the Main Divide.

It could also explain the presence of Nothofagus solandri as an important species in Eastern Fiordland and in Western Fiordland but not in Central Fiordland. Under the conditions of lower rainfall in Eastern Fiordland, Nothofagus solandri has certain advantages over the other major tree species in the area, silver beech. In Central

Fiordland, however the higher rainfall makes for an improvement in conditions for forest growth, and consequently silver beech becomes more widespread at the expense of Nothofagus solandri. Further west, however, the country becomes much steeper, the areas of weakly weathered rock and sites of poor drainage become more extensive and consequently the sites available for Nothofagus solandri again increase. On the Fiord Walls, in Western Fiordland, Nothofagus solandri can grow right at sea level with its foliage overhanging salt water. It can survive here as competition from other forest species is kept low by repeated landslides which prevent the development of anything but a seral vegetation.

It has been mentioned that the highest bushlines in the country are in the Branch and Leatham tributaries of the Wairau River and on the western and southern faces of Mt Ruapehu, and that these bushlines are dominated solely by Nothofagus solandri. On moving south from Mt Ruapehu, in the North Island, through the Northern and Central Ruahine Ranges, the altitude of the bushline rapidly descends and eventually it becomes dominated by species other than Nothofagus solandri. Kamahi is the bushline species in the proximity of the Manawatu Gorge while in the southern ranges of the North Island, silver beech is the bushline species. In the South Island much the same pattern is apparent on moving towards the north and west coasts from Central Marlborough, and on moving towards the west and south coasts from central Eastern Fiordland. Again the altitude attained by Nothofagus solandri falls off rapidly. Again the bushlines become depressed and dominated by silver beech and sometimes, as in the central Paparoa Range, and in the central regions of the West Coast, they be-

come dominated by kamahi and southern rata. It would appear that the causes of this fall off in the importance of Nothofagus solandri at high altitudes are related in some way to distance from the coast. However, whatever these factors are they affect different species in different ways. For instance the upper levels of silver beech and red beech are not depressed to nearly the same extent as is Nothofagus solandri. Kamahi seems to be hardly depressed at all, and in each case the fall off in importance of Nothofagus solandri is paralleled by an increase in the density and extent of the subalpine scrub belt. Zotov (1938) and Elder (1965) have related such changes in the composition of the vegetation to increase in cloud and fog and a resultant decrease in insolation. Certainly the fall-off in the altitudes attained by Nothofagus solandri appears to be paralleled by increase in rain and fog and presumably by a decrease in insolation, but information on these climatic factors is largely lacking for the areas under consideration. If insolation is the important factor in causing this depression of Nothofagus solandri, it would be expected that shade tolerant species would be less affected by proximity to coast than light demanding species. There is some suggestion that this is in fact so. For instance kamahi is probably more shade tolerant than the beech species and it is least affected by proximity to the coast. Silver beech and red beech are probably more shade tolerant than Nothofagus solandri and they in turn are less affected than this species. However, as accurate information on the relative shade tolerances of these species is largely lacking the evidence for the role of fog must remain largely inconclusive.

The two varieties of Nothofagus solandri, mountain beech and

black beech, have in many ways similar ecological requirements. Both can tolerate conditions of low rainfall and of excess soil moisture. Neither appear capable of competing with other trees and shrubs on the better sites for forest growth, but whereas mountain beech shows a strong tolerance for conditions at high altitudes, black beech is strictly a low altitude tree. Trees which have all the characteristics of black beech can be found throughout the distribution of Nothofagus solandri in the North Island and in the northern South Island. The southern limits of this variety are at Fletchers Creek in the Inangahua drainage in the west and in the southern Seaward Kaikoura Range in the east. However, there are forms which fall intermediate between black beech and mountain beech throughout. For instance a form which has an adult leaf shape similar to black beech but a juvenile form similar to mountain beech occurs at low altitudes along the Canterbury foothills and a form which has a juvenile form similar to black beech but an adult leaf shape similar to mountain beech occurs at low altitudes in parts of Southland.

SECTION 3 THE MOUNTAIN AND BLACK BEECH ASSOCIATIONS

3.1. INTRODUCTION

It has been shown in Section 2 how Nothofagus solandri grows on wetter sites, drier sites and at higher altitudes than most other New Zealand tree species. It may well be that its ecological behaviour is different at each of these sites and information on the performance of the species such as growth rates, taken at one particular site, may be far from representative. Likewise its behaviour where it is the sole tree or shrub is likely to be different from that where it occurs as a member of a complex community. Thus in order to study the variation in the behaviour of Nothofagus solandri throughout its range of habitat, and to throw some light on the properties which allow it to exist and compete with other species on certain sites, some form of site classification is necessary.

There are two main ways in which an attempt may be made to define and subdivide the range of environment where Nothofagus solandri occurs. The first, more obvious method, is to in some way measure the various facets of the environment of a large number of sites throughout the distribution, i.e. the altitude, aspect, physiography, climate, etc. but such an approach would be difficult, in fact well nigh impossible with the facilities available, for, even assuming that the identity of all the significant factors determining the behaviour

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* In this thesis association refers to 'a group of plants that has a definite floristic composition, presents a uniformity of physiognomy, and grows under uniform conditions. (See Spurr, S.H. 1964, page 226.)

of the species on a particular site was known and the means to measure them available, there would still be no idea of how these factors interact and measurement of them would be restricted to the present without any serious regard to what they were in the past, and it is the history of a species on a site which is often important in determining its present behaviour.

The second, and in the circumstances only practical approach, is to define and classify in terms of one aspect of the environment, one which as well as being an important factor in itself, might also be expected to be an integrator of all the other factors. Probably the easiest such factor to measure would be the combination of plant species growing on a particular site. Using such an approach, the classification of the site would depend on the typing of the vegetation. All typing of forests and scrublands in this country up to date has been done on the combination of the major canopy species with little regard for the understorey. In the case of forest, most such classification procedures have been justified on the basis that the primary object has been timber utilisation. However, such a system is too insensitive for the purpose of this study in that it provides little more than a distribution pattern of the major tree species. For instance, forest in which the sole canopy species is Nothofagus solandri, and which would consequently be classified into one type, may occur at altitudes ranging from sea level to bushline, and from extremely wet to extremely dry sites. If, however, we take into consideration some of the understorey species in the classification, the range of environment becomes subdivided. Thus it may be found that near sea level the mountain beech has an understorey of

mahoe and Cyathea dealbata, both of which are absent from near bush-line, and at bushline the understorey may be of Coprosma pseudocuneata and Podocarpus nivalis, both of which are absent from near sea level. On the very wet sites the understorey may be of Dacrydium biforme and Gahnia procera both of which are absent from the very dry sites whereas on the very dry sites the understorey may include Gaultheria antipoda and Senecio haastii, both of which are absent from the very wet sites. The more species which we take into consideration, the more sensitive must become the definition of the environment.

3.2 METHOD OF CLASSIFICATION

3.2.1. Collection of Data

In the course of this study some 2400 sociological descriptions of forest and scrub in which Nothofagus solandri is present were acquired. Some 1300 of these descriptions were collected specifically for this study. Most of the remaining 1100 were borrowed from plot records from plots established by various vegetation surveys carried out by the New Zealand Forest Service i.e. Ecological Survey, Forest and Range Experiment Station Surveys and Indigenous Forest Survey. For some 300 of these 1100, I was attached to the survey teams which established the plots from which the descriptions were taken. For the remaining 800 I had no part in collecting the plot data but have managed to visit many of the areas from which it was taken. A few of the descriptions, for areas of more difficult access, have been borrowed from the note-books of various ecologists throughout the country.

These descriptions, from here on referred to as plots, have

been chosen to cover as much of the distribution and environmental range of Nothofagus solandri as was practicable, and an attempt has been made to weight the number of plots taken from an area to the importance of Nothofagus solandri in the forest or scrubland composition of that particular area. However, in some areas of difficult access, such as south-west and southern Fiordland, the coverage is definitely thinner than it should be.

The necessity to go to other sources for plot data in order to give the maximum possible coverage of the Nothofagus solandri forests and scrublands dictated that a simple form of plot measurement be adopted. Further, considering the large area over which Nothofagus solandri is a component of the forest and scrub, and considering that much of this area is of relatively difficult access, a larger number of simple plots might be expected to be more rewarding in terms of information provided than a smaller number of plots which would result from the adoption of a more complicated design.

The measurement of each plot basically consisted of a listing of the plant species composing the community and a listing of the habitat under the following headings:-

(a) Altitude above sea level, measured to the nearest 50 feet.

(b) Aspect, categorised into North, South, East, West, North-west, South-west, South-east or North-east.

(c) Slope, categorised into Flat, Gentle, Moderate or Steep depending on whether it was less than 3 degrees, between 3 degrees and 10 degrees, between 10 degrees and 30 degrees or greater than 30 degrees.

(d) Physiography categorised into Ridge, Face, Gully or Terrace.

(e) Drainage as Good, Moderate or Poor.

(f) Nature of Parent Rock.

(g) Canopy density as Open, Medium or Dense.

(h) Geographic location.

A non-area basis was employed for plot layout and all species of vascular plants which could be seen from the plot centre were recorded under the various tiers in which they occurred. The tiers were defined as tall tree, small tree, tall shrub, small shrub and ground species. Thus all tree species greater than about 40 feet in height were recorded under the tall tree tier, those occurring between 15 feet and 40 feet were recorded in the small tree tier, species between 6 feet and 15 feet in height were recorded in the tall shrub tier while those between 1 foot and 6 feet in height were allocated to the small shrub tier, and species less than 1 foot in height were recorded in the ground tier. Lianes, epiphytes, and parasites were recorded separately. After completion of the preliminary listing of all vascular species visible from the plot centre, about 10 minutes (more or less depending on the complexity of the vegetation) were spent searching for further species in the area and allotting physiognomic ratings. Three classes of physiognomy were employed i.e. dominant within tier, present within tier, and present as seedling only. Not more than three and not less than one species from each tier (except in cases of total absence of species from a tier) were recorded as being dominants, i.e. the species which in terms of cover were the most important within the tier. An estimate of the density of each tier was made under one of three categories, open, moderate, or dense. An estimate was made of the breast height

diameter range for each of the tree tiers and notes were taken on the predominant ground cover (whether it was mainly litter, bare soil, or vegetation) on the abundance of regeneration of the major tree species, and on other special features, such as presence of charcoal, indicating past burning, or the seral status of the community. The species of plants which showed indications of browse by deer, chamois, goats or opossum were recorded and an estimate made as to whether the degree of severity of browse was light, moderate or ~~dense~~ heavy.

The non-area basis of plot design fits in with the concept of minimal area (see Greig-Smith, P. 1957) and it was found that very few new species were located on a plot site once an area of approximately a tenth of an acre had been covered. In most cases the size of the plot was in fact limited by defining the environment. For instance, if the plot centre was located on a terrace, where the canopy was open, the plot area would be restricted to the terrace site and would not include adjacent slopes. Likewise it would be restricted to the stand where the canopy was open and would not include adjacent dense stands. As the Forest Service Surveys from which data was borrowed employed plots either equal to or in excess of one tenth acre, little complication in this direction resulted from their inclusion in this study. Complications did occur, however, in the lack of consistency in naming of plant species and when it came to analysis of the plot data to produce a typing of the Nothofagus solandri communities, a certain degree of detail in the identification of some of the species had to be sacrificed in order to make the plots from the various sources conform. This, fortunately, concerned mainly the minor species from the lower tiers and only in a few cases were

physiognomic dominants, or the tree and larger shrub species, involved. Thus Uncinia species could only be divided into wide or large-leaved and fine-leaved groups, and not into individual species. All cryptogams had to be grouped and are referred to as moss. Pittosporum crassicaule, Pittosporum rigidum and Pittosporum divaricatum had to be combined, the fern genus Hymenophyllum could not consistently be dealt with in terms of individual species and so the lot, with the exception of Hymenophyllum malingii, had to be grouped together. Carex species were grouped together and in most cases grasses could be allotted to a genus only. This necessity to combine the species from some genera into one taxonomic unit had certain disadvantages when it came to analysis, but there was no other alternative.

The selection of plot sites in the field was generally done in a systematic fashion. Ecological Survey and National Forest Survey plots were certainly installed systematically at regular intervals along grid lines. The plots specifically measured for this study were in most cases arranged in lines, at intervals of 200 feet along altitudinal gradients, the starting points of which were usually along stream courses and were pre-chosen on a map to give a regular distribution throughout a particular area.

3.2.2. Analysis of Data

As mentioned in the introduction to this section, it seems likely that the more species which are taken into consideration in the formation of the Nothofagus solandri associations, the more sensitive must become the classification of sites. In fact all species of vascular

plants and moss, which was treated as one taxonomic unit, were included in the analysis. However, over 550 species of vascular plant were encountered in this study (See App. 2) and they occurred in more than 2350 different combinations. Outside of eastern Southland and Canterbury, no two identical plots in terms of species composition were, in fact, encountered. Added to this large range of combinations of species is variation in their physiognomic ratings. In all there is thus potentially a very large number of different combinations. Ideally each such combination might be regarded as a separate community in itself but such large numbers of associations are impractical to deal with. The problem thus becomes one of grouping of the plots on the basis of least difference. To do this, indices of similarity between plots were employed and on the basis of the calculated indices, the plots were clustered ultimately into 23 groups. A stepwise description of the method employed follows:

(a) The plots were divided into seven groups and for every possible combination of two plots within each group an index of similarity was calculated using the formulae:

$$I = \frac{100\ (15^{d} + 6p + s)}{15d + 6p + s + 3a}$$

where d = number of species dominant in both of the plots being compared.

p = number of species above 'seedling only' status present in both plots but not present as a dominant in more than one of them

s = number of species present in both plots but occurring as a 'seedling only' in at least one of them

a = number of species present in one only of the plots being compared.

A full matrix of indices comparing each plot with each other plot was then built up separately for each group.

(b) The following procedure was adopted separately for each of the matrices built up: The matrix was searched for the highest index of similarity relating any two plots. These two plots were combined and the row and the column in the matrix for each of these plots, relating them with all other plots in the matrix, were then added together to form a single row and column which was then divided by two (the number of plots in the combination) and the resultant row and column was thus the average relationship of the combined plots with all other plots in the matrix. This process of searching for the largest index in the matrix, combining the related plots and calculating an average row and column was then repeatedly carried out and when a group of combined plots, combined with a single plot, or when two groups of uneven size came together, the row and column for each group was multiplied by the number of plots composing it. The rows and columns were then added and the new row or column was arrived at by dividing by the number of plots in the new group formed. This process was repeated until 25 to 30 discrete groups of three or more plots each remained. This occurred, in the case of each matrix, at around the 50 per cent level of similarity. The total number of such groups from the seven matrices was in fact 186 and the number of plots composing the groups ranged from three plots through to about 40 plots each. Some six per cent of the plots fell into groups which contained only one or two plots and these plots were ignored

in the next stage of the analysis - stage c.

(c) Each of the 186 groups was now treated as a single plot and an importance value was assigned to each of the species occurring in each group. This importance value incorporated both the percent frequency and the physiognomy of the species and was arrived at by assigning one point for the occurrence of a species in a group as a dominant, 0.6 of a point to each occurrence of a species present as more than a 'seedling only' but not dominant and 0.2 of a point to each species present as a seedling only, i.e. in the ratio of 5 : 3 : 1. The total points for each species in each group were then added and multiplied by 100 times the reciprocal of the number of plots in the group. Thus if a species was present as a dominant in all plots of a particular group it would receive a value of 100, but if it was present as more than a 'seedling only', but not dominant, in the plots it would only receive a value of 60 even though the percent frequency would be 100. If in a group composed of 50 plots a species occurred ten times as a dominant, fifteen times as present and five times as a 'seedling only', its importance rating for that group of plots would be

$$\frac{100\ (1 \times 10 + 0.6 \times 15 + 0.2 \times 5)}{50} = 40$$

An index of similarity was now calculated for each pair of groups of plots and a new, full matrix of 186 x 186 indices built up. In this case the index of similarity employed was Sorensen's K (see Looman, J.; Campbell, J.B. 1960):

$$k = \frac{2c}{a + b} \times 100$$

where k = Sorensen's index of similarity between two groups of plots being compared

c = sum of importance values shared between the two groups for species common to both

and a and b = the total sums of all importance values of all species in each of the two plots respectively.

Thus k = 100 when the two groups have identical species, each with identical importance ratings and k = 0 where there are no species in common.

This matrix was broken down by a cluster technique identical to that described under 'b' except that in the former case combinations initially involved one plot combining with one plot, but here all combinations involved groups of plots and this had to be taken into consideration in the recalculation of rows and columns right from the start. The clustering process was continued until the number of groups of plots had been reduced to 23. This again occurred at a level of 'k' equal to about 50. These 23 groups formed the nucleus of the Nothofagus solandri associations which are described in the following pages.

(d) An importance value was calculated for each species in each of the 23 association nuclei using again the frequency and physiognomic ratings of the species, and for each of the original 2400 plots, each species was given an importance rating based on physiognomy alone. In each plot a dominant species was given a rating of 100, a species present above seedling only status but not dominant was given a rating of 60 and a species present as seedling only was given a rating of 20. Thus the ratio of importance was still in the order

of 5 : 3 : 1. An index of similarity $k = \frac{2c}{a + b} \times 100$ was now calculated between each plot and each association nucleus. On the basis of these calculations approximately 35 per cent of the plots were rearranged into different association nuclei. New importance ratings for each species in each association nucleus were then recalculated and the process of testing each plot against each recalculated association nucleus repeated. This time only 6 per cent of the plots required rearranging, and the new groupings were accepted as being the associations for the purposes of future discussion. Importance ratings and percent frequencies were calculated for each species in each association, and on the basis of a matrix construction and cluster analysis as for that described above, a dendrogram of the relationship of the associations was constructed and the associations were numbered accordingly (see Fig. 8).

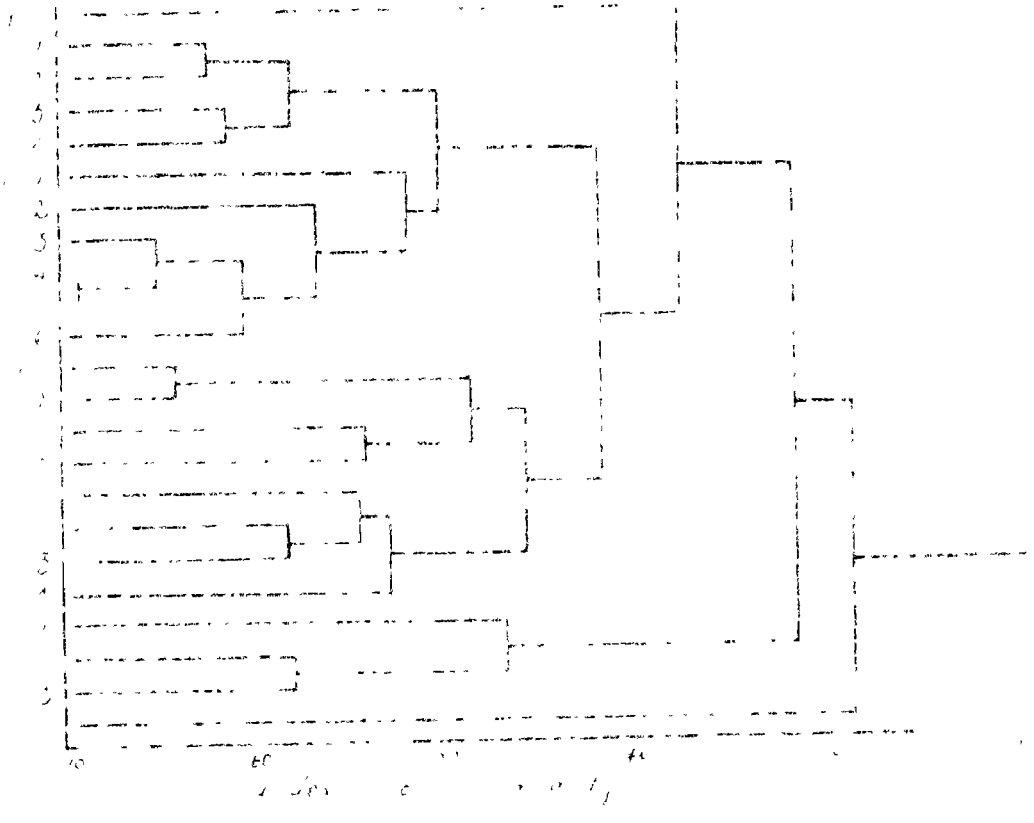


Fig. 8 - Dendrogram to show relationship of the 23 associations.

Ideally all 2400 plots should have been calculated into a single large matrix, instead of into seven smaller matrices, and this large matrix broken down directly into associations by one clustering procedure. However, with the method of clustering which was employed this matrix would have had to contain 5,760,000 elements or similarity indices and even if certain difficult modifications had been made and a half matrix instead of a full matrix had been employed, there would still have been 2,880,000 elements. The computer used for the calculation was the IBM 360 at Canterbury University and even using the full disc storage available, the maximum sized matrix which could be accommodated was one containing somewhat less than 500,000 indices. This allowed for approximately $\frac{1}{4}$ of the plots to be fed through in one operation and in fact the first batch did contain 600 plots. However with employment of disc storage for a batch of this size the time taken for the operation was prohibitive, and subsequently batches of 300 plots only were fed through. Even so the operation, and especially the clustering part of it, was a lengthy one.

The necessity to divide the plots into a number of groups before calculation of indices of similarity and cluster analysis posed two major problems. The first was how to recognise whether a particular association occurred in more than one of the groups and to solve this problem the second index of similarity 'k' was introduced and a clustering carried out on the 186 subtypes resulting from the breakdown of the seven matrices (see above under heading (c)). The second problem was one of overlap which would result from such a combination clustering. The combining of the results of the seven

clusterings must to a certain extent result in plots more closely related to one association being placed in a neighbouring association and also allow for the possibility of two identical plots being placed under different associations. To avoid this problem each plot was tested against the association nuclei (see (d) above) and rearrangement of the plots, where necessary, was carried out.

Two other points require clarification. The first relates to the relative weighting assigned to dominant species, other species, and species present as seedlings only, in the calculation of indices of similarity. The ratio of importance has been placed at 5 : 3 : 1. At first glance this ratio would appear to be attaching too much importance to species which are not physiognomic dominants and, in fact, if the only consideration in the selection of this weighting had been the influence of plant species on plant species this would be true, but the individual species, as mentioned previously, are also being used as indicators of other facets of the environment and this was taken into consideration when these arbitrary weightings were chosen.

The second point relates to the use of two indices of similarity. When the first index, which was developed for this study, was chosen it was anticipated that all plots would have been dealt with simultaneously by the computer. It was considered that the first index would be the most efficient in terms of machine time. It was also considered that the calculation of 'importance values' for the species, necessary for the application of the second index of similarity 'k', would tend to give misleading results when applied to the original plots since here they would need to be calculated purely

on the basis of physiognomy with no consideration of frequency. However, as calculation proceeded it became apparent that both arguments were largely groundless and if the analysis was repeated the second index 'k' alone would be employed. Certainly the first index 'I' had disadvantages, the most outstanding being that the weighting towards dominance is variable and though in the order of 5 : 3 : 1 where the plots being compared have an average number of species for the study, it tends to increase towards 15 : 6 : 1 as the number of species increases towards infinity, and tends to decrease towards 1 : 1 : 1 as the number of species decreases towards zero. Also, the weightings tend towards 1 : 1 : 1 as the species composition in the plots being compared approaches identity, and conversely the weighting toward physiognomy increases as the plots become more dissimilar.

3.3. THE ASSOCIATIONS

A description of the habitat and of the structure and composition of the plant community is given below for each of the 23 associations of Nothofagus solandri. The associations as mentioned previously have been defined by an objective numerical system and the allocation of the plots to associations has likewise been objective and thus there is no obvious bias in the placing of the plot.

A set procedure has been adopted for the description of each association. For each, the number of plots used in the construction of the association has been given. This is followed by a description of stand structure and composition. Under this heading there is a community diagram which presents in a graphical form the percent

frequency (open bars) and 'Importance Rating' (closed bars) of the twenty most important species in the association. Also under this heading the mean complexity, the mean height of the stand and the canopy density is given. The standard error (P = 0.05) is given for the mean complexity and mean stand height. The mean complexity represents the mean number of all vascular plant species plus moss for all plots in the association. Canopy density is described as open or dense only when the plots in the association show a strong tendency in one direction or the other. Otherwise it is described as being variable. The composition is given separately for the tree tiers, the shrub tiers, the ground tiers and the lianes, obligate epiphytes and parasites and in each case the species are separated into major species which have frequencies between 70 and 100 percent, moderate species which have frequencies between 40 and 70 percent and minor species which have frequencies between 10 and 40 percent. Species which have frequencies lower than 10 percent are ignored. The tree tiers include all plant species which commonly grow to heights greater than 15 feet in the association. The shrub tiers include the woody species which commonly grow to between 1 foot and 15 feet high plus non-woody species that form a definite trunk and grow to heights greater than 1 foot but less than 15 feet high. The ground tiers include all non-woody species which do not form trunks and woody species which do not usually grow taller than 1 foot in height. Some indication of the usual density of the lower tiers is given. The density of the upper tier can be deduced from the record of canopy density.

The habitat of each association is described under the headings

'area', 'altitude' and 'physiography'. The 'area' breakdown into North Island, Northern and Western South Island, Eastern South Island, and Southern South Island is that defined and used in Section 2. The number of plots which fall into each area is recorded and the location of the plots is described. The range of altitude for each association has been calculated from the altitude of all the individual plots within the association and represents a range of one standard deviation around the mean (i.e. 67% of the population). Where an association is important in more than one of the areas, the range of altitude is given for each. Any strong preference of an association for terrace, face, spur and gully sites, for flat, gentle, moderate or steep slopes, for poor soil drainage, for particular rock or for particular soil condition is given under the heading of physiography. For tabulated detail on canopy density and physiography for each association see App. 3.

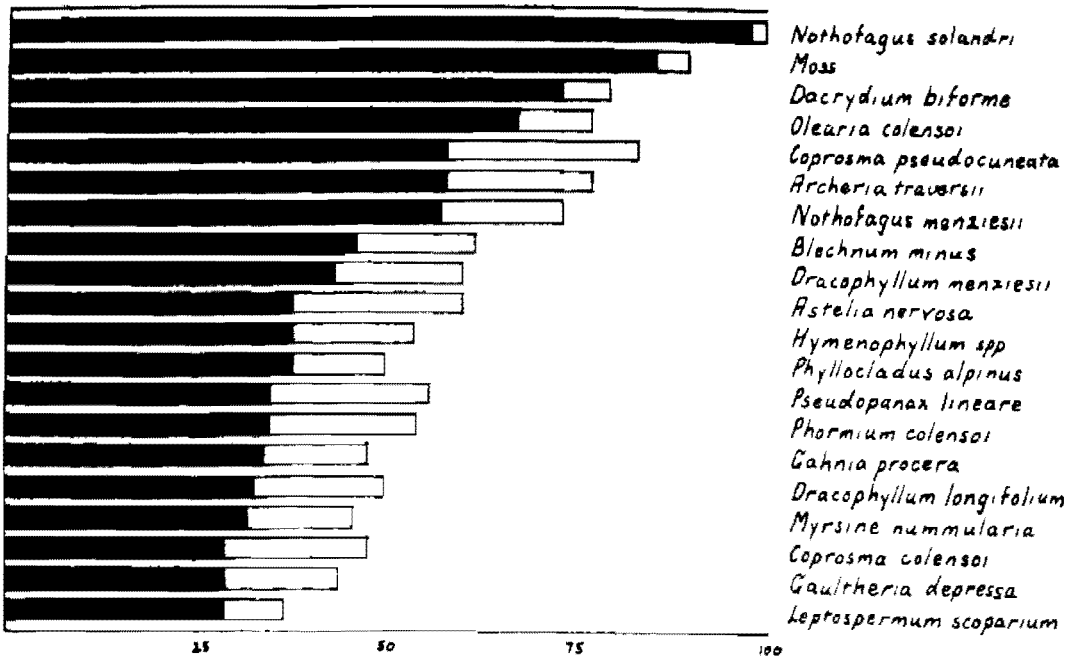
The description for each association is as follows:-

Association A 1

No. of plots: 57

Stand Structure and Composition

Community diagram:



Mean Complexity: 23.4 $\pm$ 1.8 (P = 0.05) species

Mean Stand Height: 17.4 $\pm$ 3.4 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Usually absent. If present the main species are Nothofagus solandri (mountain beech) and Nothofagus menziesii.

Shrub Tiers: Dense.

Major Species: Nothofagus solandri, Coprosma pseudocuneata, Dacrydium biforme, Archeria traversii, Olearia

colensoi, Nothofagus menziesii.

Moderate Species: Dracophyllum menziesii, Pseudopanax lineare, Phormium colensoi, Phyllocladus alpinus, Dracophyllum longifolium, Coprosma colensoi, Cyathodes juniperina, Myrsine divaricata.

Minor Species: Leptospermum scoparium, Coprosma foetidissima, Dracophyllum uniflorum, Metrosideros umbellata, Pseudopanax colensoi, Pseudopanax simplex, Pimelea gnidia, Pittosporum (small leaved spp), Senecio bennettii.

Fig. 9 - Association A 1, Lake Mike, South-western Fiordland. This is a low growing association occupying sterile rock surfaces and areas of poor soil drainage.
Note: Olearia colensoi in the understorey.

Ground Tiers: Dense.

Major Species: Moss.

Moderate Species: Blechnum minus, Astelia nervosa, Hymenophyllum spp., Gahnia procera, Gaultheria depressa, Myrsine nummularia, Chionochloa acicularis.

Minor Species: Astelia linearis, Forstera sedifolia, Enargia parviflora, Grammitis billardieri, Pentachondra pumila, Uncinia (fine leaved spp.), Drosera stenopetala, Schoenus pauciflorus.

Habitat

Area:

North Island: 5 plots. Rare occurrence in Raukumara, Huirau and Ruahine Ranges.

Northern and Western South Island: 14 plots. Moderately common but confined to the Western side.

Eastern South Island: 0 Plots.

Southern South Island: 38 Plots. An important association on the Western side of Fiordland.

Altitude: 2044-3268 feet. Mainly confined to near bushline. In the North Island it is restricted to above 4200 feet.

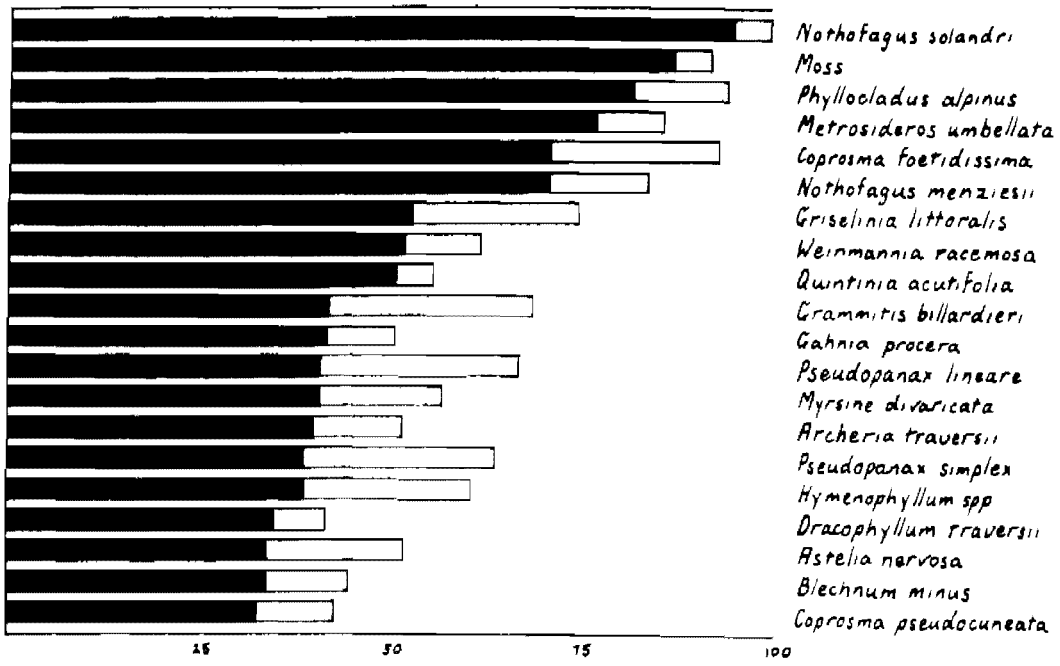
Physiography: Usually confined to faces and spurs where the parent rock is slow weathering and relatively infertile. Soil development is often confined to rock crevices. It may also occur on areas of poor drainage towards the upper limits of forest.

Association B 1

No. of plots: 141

Stand Structure and Composition

Community diagram:



Mean Complexity: 22.6 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 42.4 $\pm$ 2.4 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Meterosideros umbellata, Nothofagus menziesii, Griselinia littoralis.

Moderate Species: Weinmannia racemosa, Quintinia acutifolia, Elaeocarpus hookerianus.

Minor Species: Libocedrus bidwillii, Podocarpus hallii, Nothofagus fusca.

Shrub Tiers: Dense.

Major Species: Phyllocladus alpinus, Coprosma foetidissima.

Moderate Species: Pseudopanax lineare, Pseudopanax simplex, Myrsine divaricata, Archeria traversii, Coprosma pseudocuneata, Dracophyllum traversii, Pittosporum (small leaved spp.).

Minor Species: Coprosma colensoi, Cyathodes fasciculata, Dacrydium biforme, Coprosma banksii, Neomyrtus pedunculata, Pseudowintera colorata.

Ground Tiers: Moderate density.

Major Species: Moss.

Moderate Species: Grammitis billardieri, Hymenophyllum spp., Gahnia procera, Astelia nervosa, Blechnum minus, Libertia pulchella, Uncinia (fine leaved spp.), Enargia parviflora.

Minor Species: Blechnum capense, Blechnum discolor.

Lianes, Epiphytes etc.:

Minor Species: Asplenium flaccidum.

Habitat

Area:

North Island: 0 Plots.

Northern and Western South Island: 121 plots. An important association in the Grey catchment and in the lower Buller catchment and extending northwards to the Wakamarama Range. It extends eastwards as far as the Pelorus valley where it occurs in the proximity of the mineral belt.

Eastern South Island: 0 Plots.

Southern South Island: 20 Plots. Moderately important in Western Fiordland.

Altitude: 1930-3078 feet. Seldom extends to bushline.

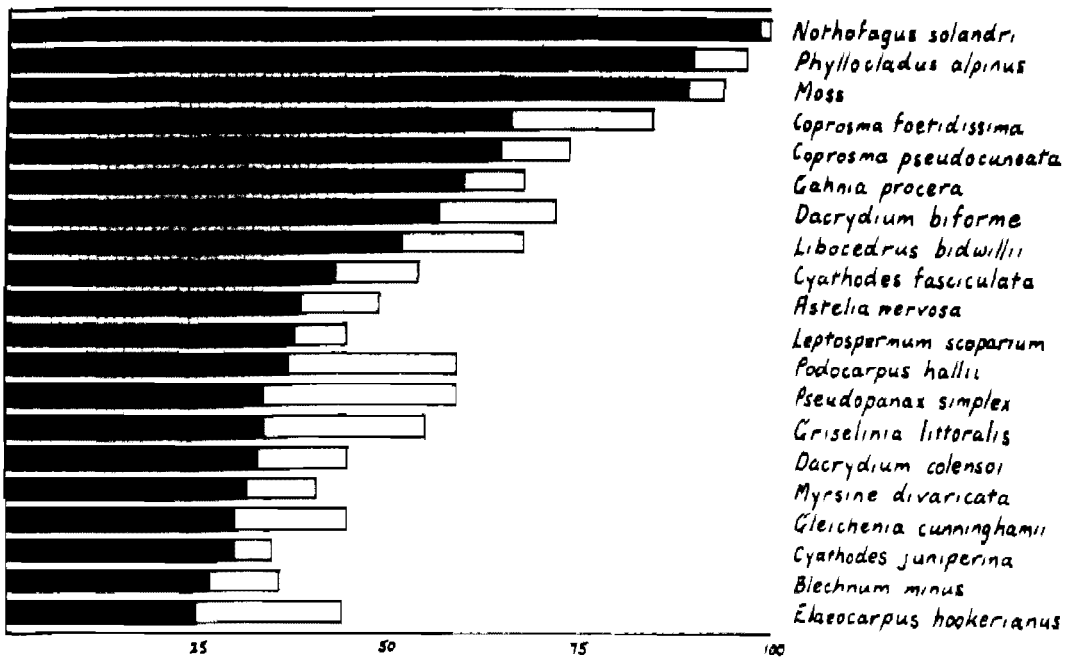
Physiography: By and large it is restricted to moderately steep to steep slopes and spurs. It does not occur on areas of poor drainage but is often present on sterile rock surfaces.

Association B 2

No. of Plots: 78

Stand Structure and Composition

Community diagram:



Mean Complexity: 18.6 $\pm$ 1.1 (P = 0.05) species

Mean Stand Height: 37.3 $\pm$ 2.8 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech) Dacrydium biforme.

Moderate Species: Libocedrus bidwillii, Podocarpus hallii, Griselinia littoralis, Dacrydium colensoi, Leptospermum scoparium, Elaeocarpus hookerianus.

Minor Species: Dacrydium intermedium, Nothofagus menziesii.

Fig. 10 - Association B 2, Fletcher Creek. This is an important association in areas which are poorly drained. The dominant tree species are mountain beech, Dacrydium biforme, mountain cedar and hall's totara.

Shrub Tiers: Dense.

Major Species: Phyllocladus alpinus, Coprosma foetidissima, Coprosma pseudocuneata.

Moderate Species: Pseudopanax simplex, Cyathodes fasciculata, Cyathodes juniperina, Myrsine divaricata.

Minor Species: Neomyrtus pedunculata, Pseudopanax crassifolium, Coprosma parviflora, Coprosma colensoi, Pseudopanax anomolum.

Ground Tiers: Dense.

Major Species: Moss (often sphagnum).

Moderate Species: Gahnia procera, Astelia nervosa.

Minor Species: Blechnum minus, Gleichenia cunninghamii, Grammitis billardieri, Uncinia (fine leaved spp.), Enargea parviflora, Gleichenia circinata.

Habitat

Area:

North Island: 42 Plots. Common around the west and south side of Mt Ruapehu, but does occur to a limited extent on the eastern side of Mt Ruapehu and rare stands may be found in the Kaimanawa and Northern Ruahine Ranges.

Northern and Western South Island: 32 Plots. Scattered throughout from the Pikikiruna Range westwards towards the coast and southwards to the Taramakau River.

Eastern South Island: 3 Plots. Sporadic occurrence near the headwaters of some of the major rivers where these lie close to the Main Divide.

Southern South Island: 1 Plot. From near the Hump Range.

Altitude: 1709-3857 feet. The range in the North Island is higher than in the South Island i.e. in the North Island it is from 3088-3962 feet, and in the South Island it is from 448-3048 feet.

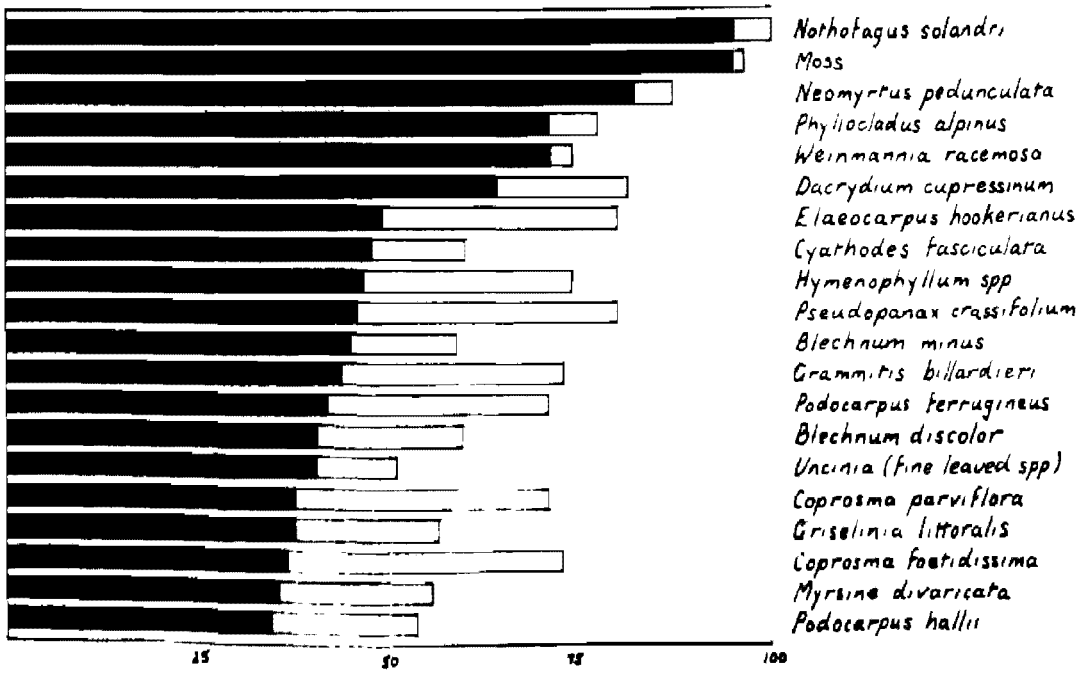
Physiography: Almost entirely confined to areas of poor drainage where the slope is flat or gentle.

Association B 3

No. of Plots: 70

Stand Structure and Composition:

Community diagram:



Mean Complexity: 26.3 $\pm$ 1.7 (P = 0.05) species

Mean Stand Height: 56.0 $\pm$ 3.0 (P = 0.05) feet

Canopy Density: Dense

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (generally mountain beech, rarely black beech), Dacrydium cupressinum, Elaeocarpus hookerianus, Pseudopanax crassifolium, Weinmannia racemosa, Griselinia littoralis, Podocarpus ferrugineus.

Moderate Species: Podocarpus hallii.

Minor Species: Nothofagus fusca, Nothofagus menziesii, Libocedrus bidwillii, Quintinia acutifolia, Podocarpus dacrydioides, Dacrydium colensoi, Metrosideros umbellata, Nothofagus truncata, Leptospermum scoparium.

Fig. 11 - Association B 3, Grey Valley. This association occupies terraces where the drainage tends to be poor. Mountain beech, rimu and kamahi are the important tree species and Neomyrtus pedunculata is nearly always present in the understorey. In this particular case mountain cedar is present.

Shrub Tiers: Dense.

Major Species: Neomyrtus pedunculata, Phyllocladus alpinus, Coprosma foetidissima.

Moderate Species: Cyathodes fasciculata, Coprosma parviflora, Myrsine divaricata, Pseudopanax simplex.

Minor Species: Coprosma colensoi, Dicksonia squarrosa, Pseudowintera colorata, Coprosma rhamnoides.

Ground Tiers: Dense.

Major Species: Moss, Hymenophyllum spp., Grammitis billardieri.

Moderate Species: Uncinia (fine leaved spp.), Blechnum minus, Blechnum discolor, Enargea parviflora, Libertia pulchella.

Minor Species: Nertera dichondraefolia, Microlaena avenacea, Nertera depressa.

Lianes, epiphytes, etc.:

Minor Species: Grammitis heterophylla, Asplenium flaccidum.

Habitat

Area:

North Island: 4 Plots. Throughout but rare.

Northern and Western South Island: 49 Plots. Common in the lower Grey catchment and in the Inangahua tributary of the Buller River but occasional stands occur throughout the rest of the area.

Eastern South Island: 3 Plots. Rare but widely distributed.

Southern South Island: 14 Plots. Moderately common from eastern Fiordland through to Beaumont but rare in western Fiordland.

Altitude: 452-1680 feet.

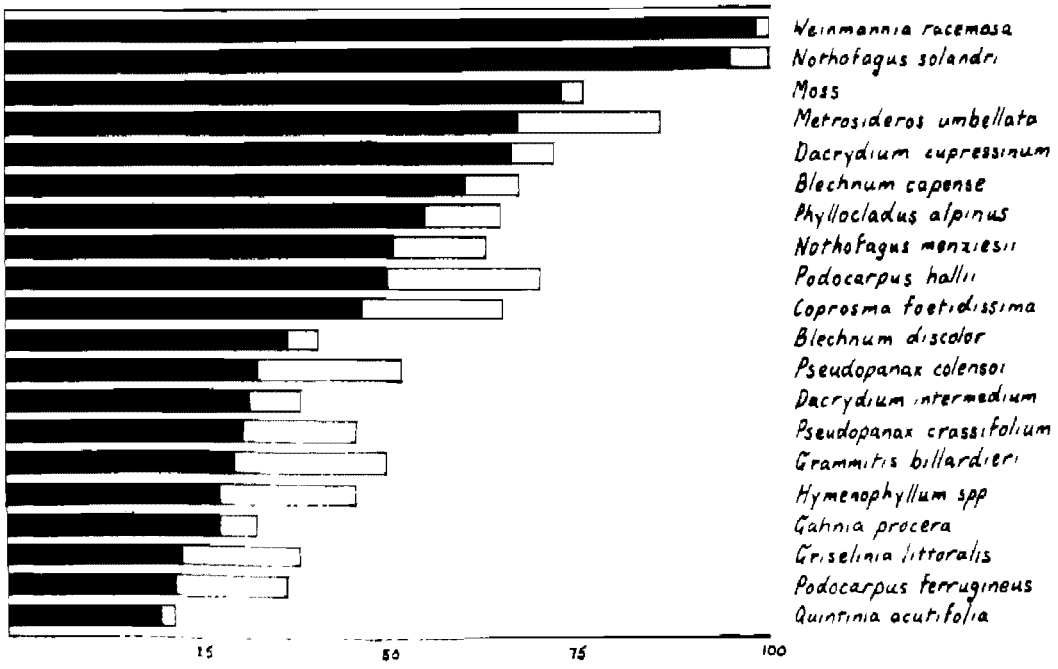
Physiography: This association is nearly always confined to areas which are flat or have a gentle slope only. The drainage is usually moderately poor to poor.

Association B 4

No. of Plots: 46

Stand Structure and Composition

Community diagram:



Mean Complexity: 21.0 $\pm$ 2.5 (P = 0.05) species

Mean Stand Height: 54.8 $\pm$ 8.4 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Weinmannia racemosa, Nothofagus solandri (mountain beech), Metrosideros umbellata, Dacrydium cupressinum, Podocarpus hallii.

Moderate Species: Nothofagus menziesii, Pseudopanax colensoi, Pseudopanax crassifolium.

Minor Species: Dacrydium intermedium, Griselinia littoralis, Podocarpus ferrugineus, Quintinia acutifolia,

Elaeocarpus hookerianus, Myrsine salicina, Myrsine australis.

Shrub Tiers: Moderate density.

Major Species: Nil.

Moderate Species: Phyllocladus alpinus, Coprosma foetidissima.

Minor Species: Coprosma lucida, Coprosma colensoi, Coprosma parviflora, Neomyrtus pedunculata, Cyathodes juniperina, Phormium colensoi.

Ground Tiers: Dense.

Major Species: Moss.

Moderate Species: Blechnum capense, Grammitis billardieri, Hymenophyllum spp., Blechnum discolor.

Minor Species: Gahnia procera, Astelia nervosa, Gleichenia cunninghamii, Lycopodium volubile.

Lianes, epiphytes, etc.:

Minor Species: Asplenium flaccidum.

Habitat

Area:

North Island: 0 Plots.

Northern and Western South Island: 10 Plots. Confined to the northern and southern ends of the Paparoa Range and to the western side of the northern extensions of the Paparoa Range, north of the Buller River.

Eastern South Island: 0 Plots.

Southern South Island: 36 Plots. An important type in the lower Arawhata and Waita catchments, and though it does extend around Western and Southern Fiordland, it is generally confined

close to the Coast.

Altitude: 246-1344 feet.

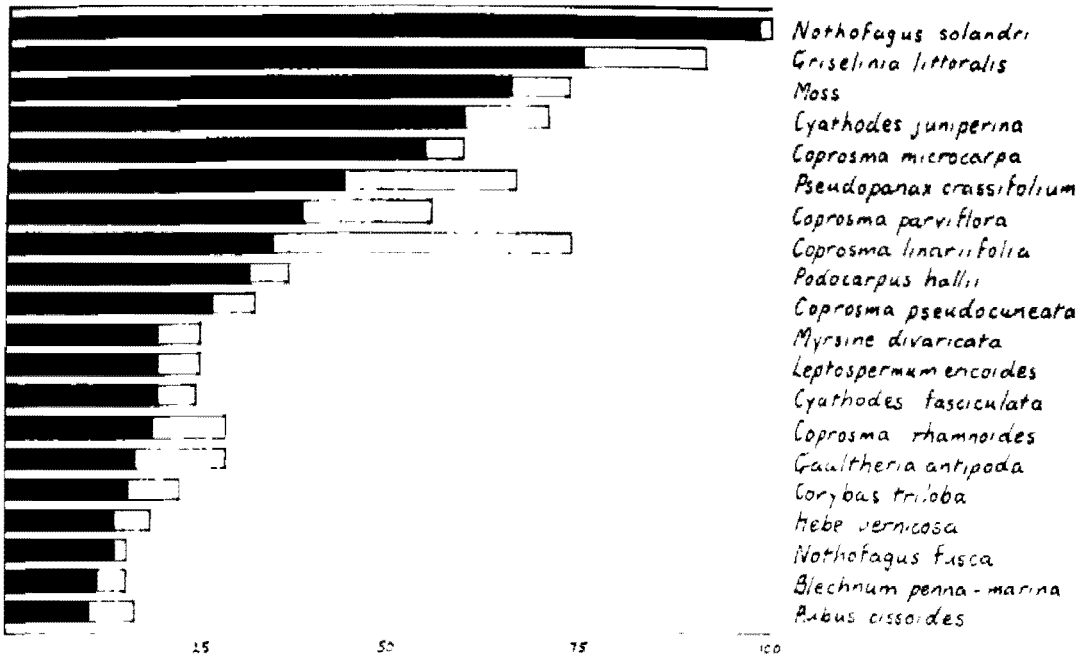
Physiography: Occurs on areas of moderately poor drainage or where there is infertile parent rock close to the surface.

Association C 1

No. of Plots: 87

Stand Structure and Composition

Community diagram:



Mean Complexity: 14.1 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 48.0 $\pm$ 3.7 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech, rarely black beech), Griselinia littoralis, Coprosma

linariifolia.

Moderate Species: Pseudopanax crassifolium.

Minor Species: Podocarpus hallii, Leptospermum ericoides, Carpodetus serratus, Nothofagus fusca.

Shrub Tiers: Moderate density.

Major Species: Cyathodes juniperina.

Moderate Species: Coprosma microcarpa, Coprosma parviflora.

Minor Species: Coprosma pseudocuneata, Coprosma rhamnoides, Gaultheria antipoda, Myrsine divaricata, Cyathodes fasciculata, Hebe vernicosa, Pittosporum (small leaved species).

Ground Tiers: Open.

Major Species: Moss.

Moderate Species: Nil.

Minor Species: Corybas triloba, Blechnum penna-marina.

Lianes, epiphytes, etc.:

Minor Species: Rubus cissoides.

Habitat

Area:

North Island: 4 Plots. Rare and restricted to the central region in the vicinity of the Kaimanawa and Kaweka Ranges.

Northern and Western South Island: 12 Plots. Occasional only on the eastern side from the Gordon Range towards the Wairau River.

Eastern South Island: 67 Plots. Important along the Canterbury foothills, in the Rangitata catchment, in the Rakaia catchment and

in the Wairau catchment. It is present to a limited extent along the east coast from the Seaward Kaikoura Range to Motunau.

Southern South Island: 4 Plots. Rare on the eastern side to as far south as the Eyre mountains.

Altitude: 1762-3066 feet.

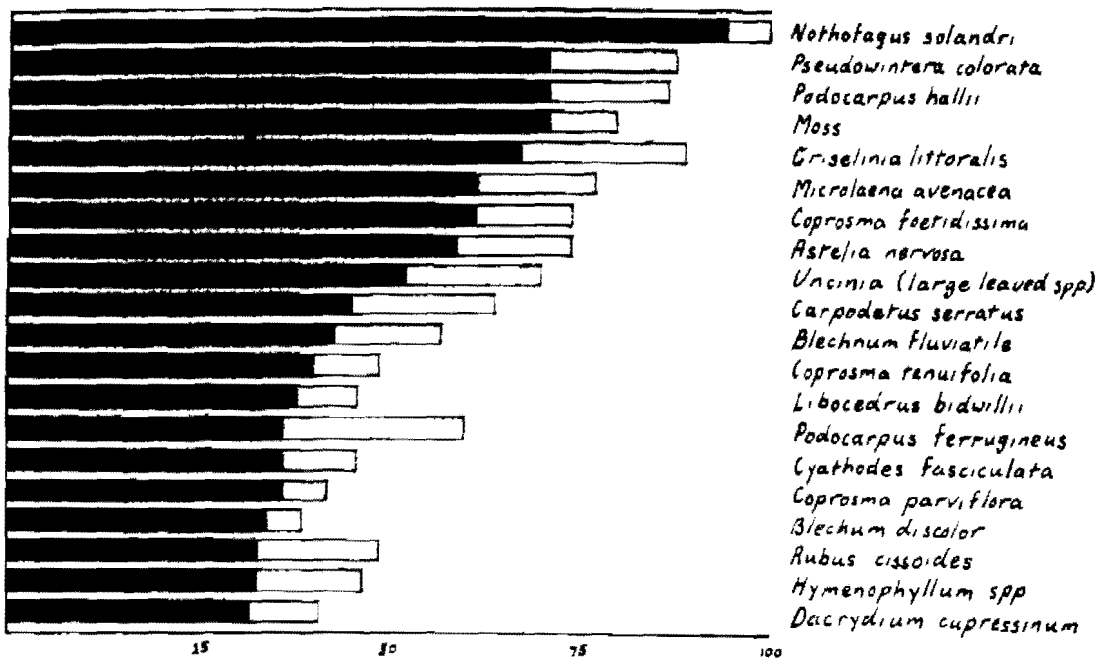
Physiography: Mainly confined to steeper slopes on faces and spurs in areas of good drainage.

Association C 2

No. of Plots: 90

Stand Structure and Composition

Community diagram:



Mean Complexity: 26.1 $\pm$ 1.5 (P = 0.05) species

Mean Stand Height: 66.5 $\pm$ 4.1 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (either black beech or mountain beech), Griselinia littoralis, Podocarpus hallii.

Moderate Species: Carpodetus serratus, Podocarpus ferrugineous, Libocedrus bidwillii, Dacrydium cupressinum, Elaeocarpus hookerianus, Pseudopanax crassifolium.

Minor Species: Pseudopanax simplex, Weinmannia racemosa, Nothofagus fusca, Dacrydium colensoi, Cordyline indivisa, Pseudopanax arboreum, Podocarpus dacrydioides, Podocarpus spicatus, Melicytus ramiflorus, Nothofagus menziesii.

Shrub Tiers: Dense.

Major Species: Pseudowintera colorata, Coprosma foetidissima.

Moderate Species: Coprosma tenuifolia, Cyathodes fasciculata, Coprosma parviflora.

Minor Species: Aristotelia serrata, Myrsine divaricata, Neomyrtus pedunculata, Phyllocladus alpinus, Coprosma colensoi, Coprosma rhamnoides, Cyathea smithii, Brachyglottis repanda.

Ground Tiers: Dense.

Major Species: Moss, Microlaena avenacea, Astelia nervosa, Uncinia (large leaved spp.).

Moderate Species: Blechnum fluviatile, Hymenophyllum spp.

Minor Species: Blechnum discolor, Polystichum vestitum, Blechnum minus, Blechnum capense, Histiopteris incisa,

Grammitis billardieri, Phymatodes diversifolium, Todea superba, Todea hymenophylloides, Uncinia (fine leaved spp.), Gahnia procera, Dicksonia lanata.

Lianes, epiphytes, etc.:

Moderate Species: Rubus cissoides.

Minor Species: Asplenium flaccidum, Parsonsia spp.

Fig. 12 - Association C 2, Western Ruapehu. This association usually occurs in areas which are flat or have gentle slope and where drainage tends to be poor. It is a tall association and has a high Podocarp element.

Habitat

Area:

North Island: 83 Plots. This is an important association in

the central North Island from the western side of Mt Ruapehu and the south of Lake Taupo through to the eastern side of the Ruahine Range. It also occurs as far north as Tauhara Peak and the southern Huiarau Range.

Northern and Western South Island: 6 Plots. Rare occurrences mainly in the vicinity of the Takaka and Motueka Rivers.

Eastern South Island: 0 Plots.

Southern South Island: 1 Plot, of marginal affinities from near the Hump Range.

Altitude: 1986-3314 feet.

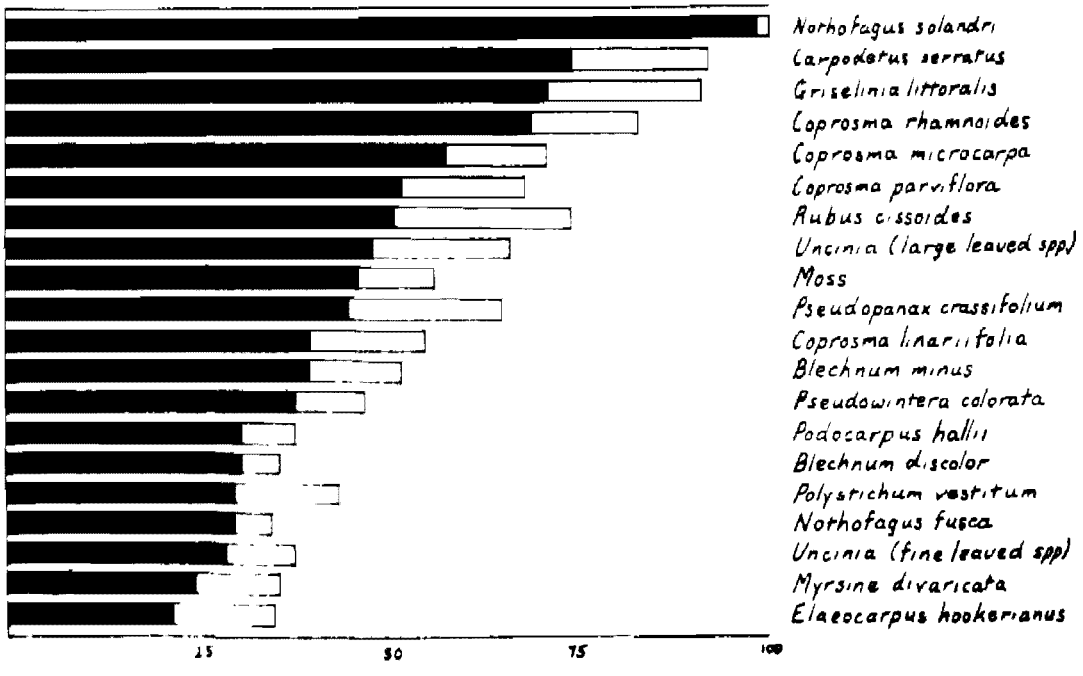
Physiography: Usually occurs on areas which are flat or have gentle slope and where soil drainage tends to be poor.

Association C 3

No. of Plots: 85

Stand Structure and Composition

Community diagram:



Mean Complexity: 22.0 $\pm$ 1.6 (P = 0.05) species

Mean Stand Height: 56.6 $\pm$ 5.5 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech or occasionally black beech), Carpodetus serratus, Griselinia littoralis.

Moderate Species: Pseudopanax crassifolium, Coprosma linariifolia.

Minor Species: Podocarpus hallii, Elaeocarpus hookerianus, Nothofagus fusca, Pseudopanax colensoi, Pseudopanax simplex, Nothofagus menziesii, Leptospermum ericoides, Fuchsia excorticata, Dacrydium cupressinum, Podocarpus ferrugineus, Pittosporum tenuifolium, Leptospermum scoparium.

Shrub Tiers: Moderate density.

Major Species: Coprosma rhamnoides, Coprosma microcarpa.

Moderate Species: Coprosma parviflora, Pseudowintera colorata.

Minor Species: Myrsine divaricata, Cyathodes juniperina, Gaultheria antipoda, Cyathodes fasciculata, Aristotelia serrata, Coprosma colensoi, Coprosma foetidissima, Neomyrtus pedunculata, Pseudopanax anomalum, Coprosma lucida, Coprosma pseudocuneata.

Ground Tiers: Moderate density.

Major Species: Nil.

Moderate Species: Uncinia (large leaved spp.),

moss, Blechnum minus, Polystichum vestitum.

Minor Species: Uncinia (fine leaved spp.), Blechnum discolor, Blechnum penna-marina, Blechnum fluviatile, Blechnum capense, Astelia nervosa, Microlaena avenacea, Carex spp., Grammitis billardieri, Corybas triloba, Phymatodes diversifolium, Acaena anserinifolia, Nertera dichondraefolia.

Lianes, epiphytes, etc.:

Major Species: Rubus cissoides.

Minor Species: Parsonsia spp. Clematis paniculata.

Habitat

Area:

North Island: 16 Plots. Scattered occurrence throughout the central regions from western Ruapehu and southern Huiarau Range through to the north-western Ruahine Range. It is most important in the southern Kaimanawa and southern Kaweka Ranges.

Northern and Western South Island: 12 Plots. Scattered occurrence throughout the Motueka and Pelorus catchments.

Eastern South Island: 53 Plots. An important association throughout the Canterbury foothills, and in the Kaikoura Range but it also occurs in the Port Hills. It has a rare occurrence in the Wilberforce, Hurunui, Waiau and Wairau catchments.

Southern South Island: 4 Plots. Rare occurrence in the Eyre mountains, and in the vicinity of Lake Wakatipu, and also near Beaumont.

Altitude: 1240-2722 feet.

Physiography: Fairly strong affinity for gentler slopes and

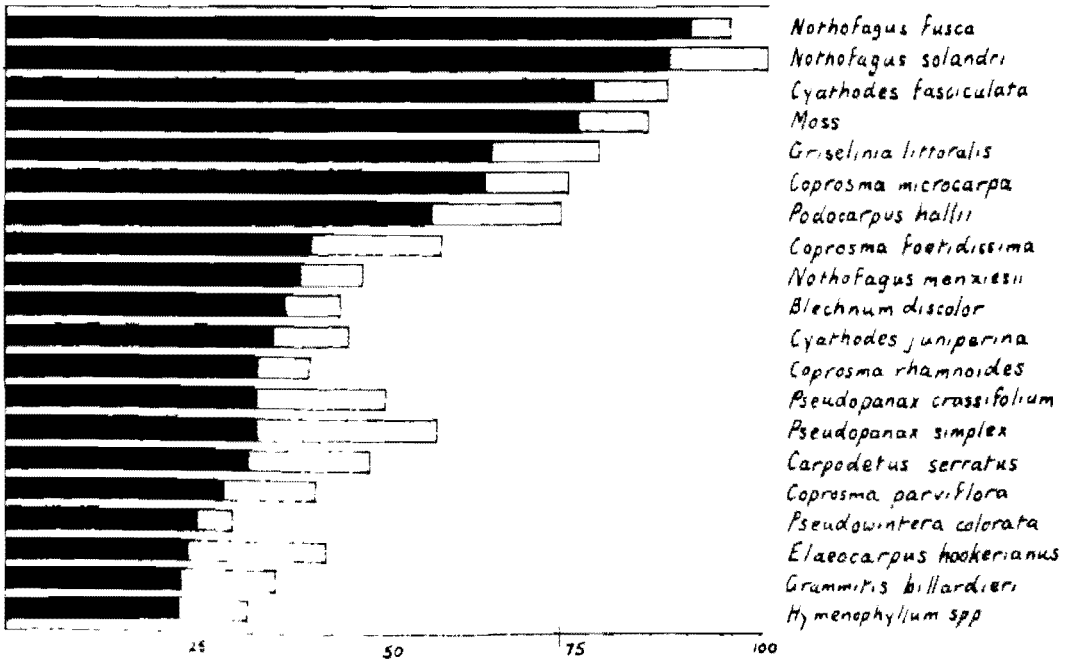
terrace sites where soil damage is moderately free.

Association C 4

No. of Plots: 115

Stand Structure and Composition

Community diagram:



Mean Complexity: 19.6 ± 1.2 (P = 0.05) species

Mean Stand Height: 63.0 ± 3.5 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech, occasionally black beech), Nothofagus fusca, Griselinia littoralis, Podocarpus hallii.

Moderate Species: Pseudopanax simplex, Pseudopanax crassifolium, Carpodetus serratus, Nothofagus

menziesii, Elaeocarpus hookerianus.

Minor Species: Coprosma linariifolia, Leptospermum ericoides, Weinmannia racemosa, Dacrydium cupressinum, Podocarpus ferrugineus.

Shrub Tiers: Moderate density.

Major Species: Cyathodes fasciculata, Coprosma microcarpa.

Moderate Species: Coprosma foetidissima, Cyathodes juniperina, Coprosma parviflora, Coprosma rhamnoides.

Minor Species: Pseudowintera colorata, Gaultheria antipoda, Myrsine divaricata, Neomyrtus pedunculata, Phyllocladus alpinus, Pseudopanax anomalum, Coprosma pseudocuneata, Coprosma colensoi, Aristotelia serrata, Olearia furfuracea, Coprosma banksii.

Ground Tiers: Moderate density.

Major Species: Moss.

Moderate Species: Blechnum discolor, Grammitis billardieri, Hymenophyllum spp.

Minor Species: Blechnum minus, Uncinia (large leaved spp.), Blechnum fluviatile, Blechnum vulcanicum.

Lianes, epiphytes, etc.:

Minor Species: Rubus cissoides, Asplenium flaccidum.

Habitat

Area:

North Island: 68 Plots. An important association in the Kaweka, Kaimanawa and Ruahine Ranges. Occasionally occurs in the

vicinity of Mt Ruapehu.

Northern and Western South Island: 43 Plots. Important east of the Tasman Range and south into the Buller headwaters.

Eastern South Island: 2 Plots. In the north but very rare.

Southern South Island: 2 Plots, both of marginal affinities and both from the Beaumont area.

Altitude: 1843-3247 feet. In the North Island the range is from 2397-3353 feet whereas in the north and western South Island it is from 1655-2697 feet.

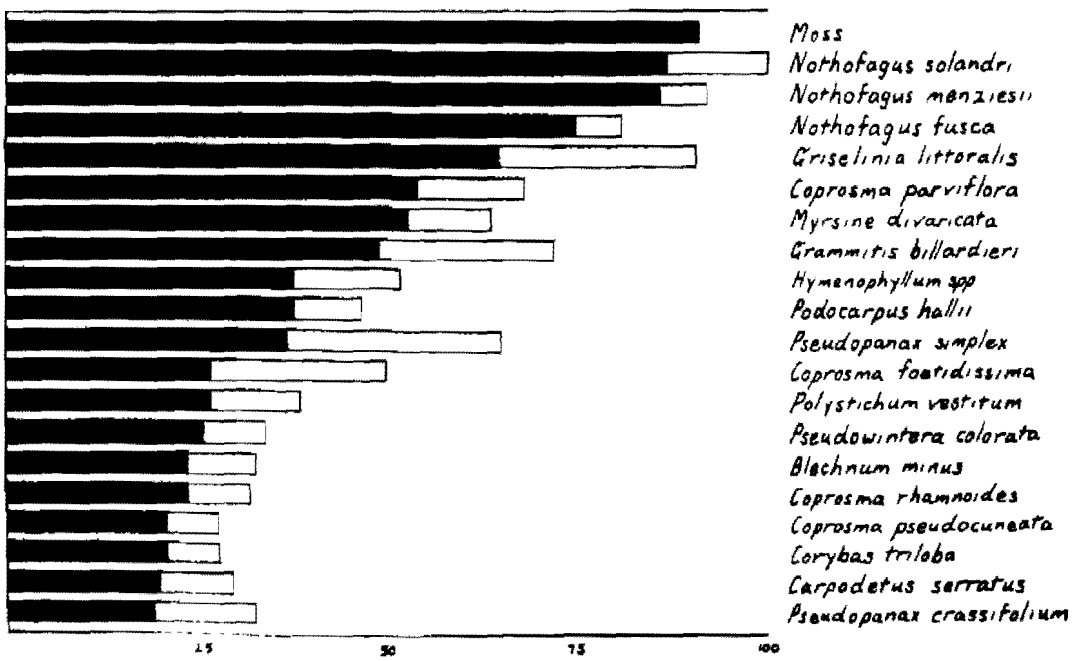
Physiography: Variable, but does not occur in areas of poor drainage.

Association C 5

No. of Plots: 137

Stand Structure and Composition

Community diagram:



Mean Complexity: 17.9 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 62.3 $\pm$ 2.3 (P = 0.05) feet

Canopy Density: Dense

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Nothofagus menziesii, Griselinia littoralis, Nothofagus fusca.

Moderate Species: Pseudopanax simplex, Podocarpus hallii.

Minor Species: Pseudopanax crassifolium, Carpodetus serratus, Coprosma linariifolia, Elaeocarpus hookerianus, Fuchsia excorticata, Pseudopanax colensoi.

Shrub Tiers: Moderate density.

Major Species: Nil.

Moderate Species: Coprosma parviflora, Myrsine divaricata, Coprosma foetidissima.

Minor Species: Pseudowintera colorata, Coprosma rhamnoides, Coprosma pseudocuneata, Phyllocladus alpinus, Neomyrtus pedunculata, Coprosma microcarpa, Coprosma colensoi.

Ground Tiers: Moderate density.

Major Species: Moss, Grammitis billardieri.

Moderate Species: Hymenophyllum spp.

Minor Species: Polystichum vestitum, Blechnum minus, Corybas triloba, Blechnum fluviatile, Uncinia (large leaved spp.), Blechnum discolor, Nertera dichondraefolia, Uncinia (fine leaved spp.).

Lianes, epiphytes, etc.:

Minor Species: Asplenium flaccidum, Rubus

cissoides, Elytranthe spp.

Fig. 13 - Association C 5, West Arm Lake Manapouri. Mountain beech and silver beech form a dense canopy over an open shrub tier. Note the dense moss and Hymenophyllum ground cover.

Habitat

Area:

North Island: 31 Plots. This association is scattered throughout the Raukumara, Huiarau, Kaweka, Kaimanawa and northern Ruahine Ranges, and is occasional in the vicinity of Mt Ruapehu.

Northern and Western South Island: 23 Plots. Scattered throughout the eastern side to as far south as the Grey headwaters.

Eastern South Island: 34 Plots. An important association in the Wairau, Waiau and Hurunui catchments, but has not been observed

elsewhere.

Southern South Island: 49 Plots. Quite an important type from the Hunter River southwards to Lake Hauroko on the eastern side of the Main Divide. It is also a major type in the forests of the Waikaia catchment.

Altitude: 1531-3219 feet. In the North Island the range is from 3007-3689 feet, in the northern and western South Island from 2087 to 3285 feet, in the eastern South Island from 1812 to 2884 feet and in the southern South Island from 1035 to 2229 feet. It never occurs near bushline.

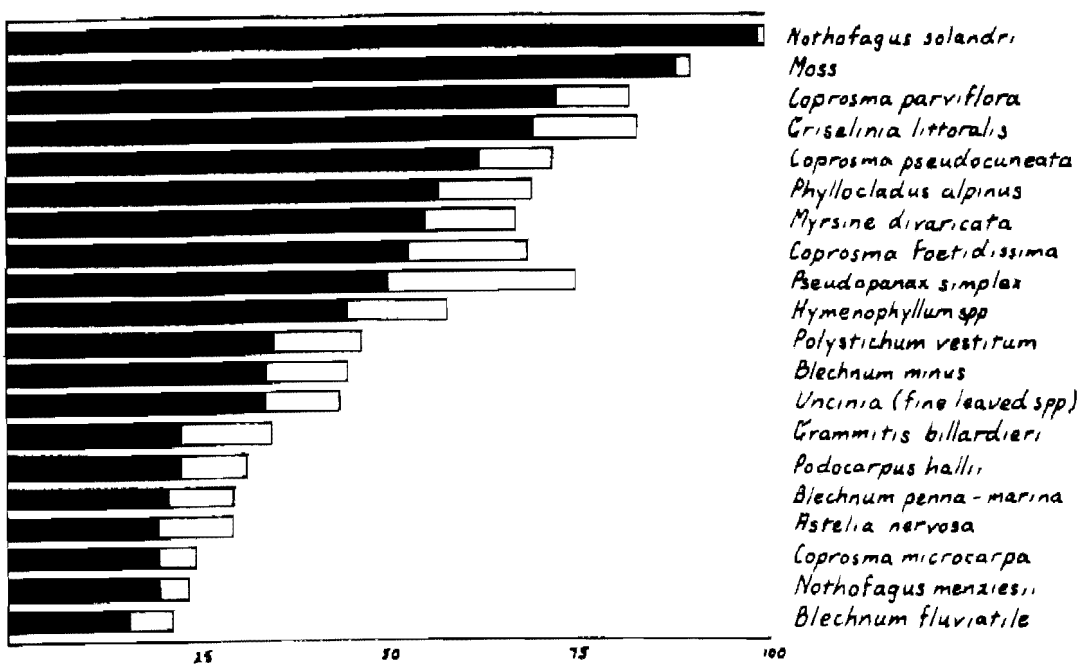
Physiography: Tends to be more important on terraces and gullies than on faces and ridge sites. Tends to occupy the more gentle slopes and flat areas provided that drainage is free.

Association C 6

No. of Plots: 200

Stand Structure and Composition

Community diagram:



Mean Complexity: 17.7 $\pm$ 1.0 (P = 0.05) species

Mean Stand Height: 49.2 $\pm$ 2.2 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Griselinia littoralis.

Moderate Species: Nil.

Minor Species: Podocarpus hallii, Nothofagus menziesii, Nothofagus fusca, Libocedrus bidwillii.

Shrub Tiers: Moderate density.

Major Species: Coprosma parviflora, Pseudopanax simplex, Coprosma pseudocuneata.

Moderate Species: Phyllocladus alpinus, Coprosma foetidissima, Myrsine divaricata.

Minor Species: Coprosma microcarpa, Gaultheria antipoda, Pseudopanax colensoi, Dacrydium biforme, Hebe stricta.

Ground Tiers: Moderate density.

Major Species: Moss.

Moderate Species: Hymenophyllum spp., Polystichum vestitum, Blechnum minus, Uncinia (fine leaved spp.).

Minor Species: Grammitis billardieri, Astelia nervosa, Blechnum penna-marina, Blechnum fluviatile, Uncinia (large leaved spp.), Acaena anserinfolia, Chionochloa conspicua, Nertera dichondraefolia, Corybas triloba, Histiopteris incisa, Lagenophora petiolata.

Lianes, epiphytes, etc.:

Minor Species: Rubus cissoides.

Habitat

Area:

North Island: 158 Plots. A major North Island association, especially in the Kaweka, Kaimanawa and northern and central Ruahine Ranges. It also extends northwards to Mt Hikurangi in the Raukumara Range and it is present around Mt Ruapehu.

Northern and Western South Island: 9 Plots. Rare and widely scattered stands throughout.

Eastern South Island: 18 Plots. Tends to be concentrated close to the Main Divide but is rare and widely scattered.

Southern South Island: 15 Plots. Rare and widely scattered but confined to the eastern side of the Main Divide.

Altitude: 2826-4180 feet. Often close to the bushline in the North Island but in the South Island it tends to be depressed and the range for the South Island plots is from 1925 to 3155 feet.

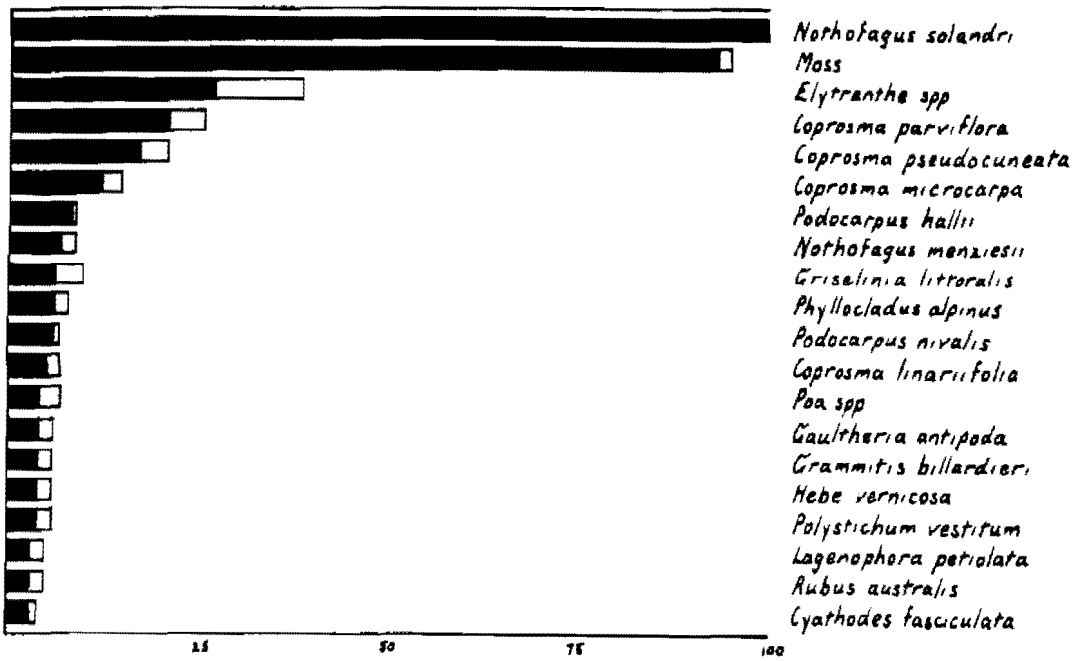
Physiography: Occurs on a range of sites but is absent from areas of poor drainage.

Association D 1

No. of Plots: 288

Stand Structure and Composition

Community diagram:



Mean Complexity: 5.2 $\pm$ 0.3 (P = 0.05) species

Mean Stand Height: 44.1 $\pm$ 1.6 (P = 0.05) feet

Canopy Density: Dense

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech).

Moderate Species: Nil.

Minor Species: Griselinia littoralis.

Shrub Tiers: Open.

Major Species: Nil.

Moderate Species: Nil.

Minor Species: Coprosma parviflora, Coprosma pseudocuneata, Coprosma microcarpa.

Ground Tiers: Open.

Major Species: Moss.

Moderate Species: Nil.

Minor Species: Nil.

Lianes, epiphytes, etc.:

Minor Species: Elytranthe spp.

Habitat

Area:

North Island: 17 Plots. Mainly in the Kaimanawa and Kaweka Ranges, but occasional stands occur in the southern Huiarau Range in the vicinity of Mt Ruapehu.

Northern and Western South Island: 15 Plots. Confined mainly to the north-east, i.e. between the Tasman Mountains and the north bank of the Wairau. Occasional stands occur in the Buller headwaters.

Eastern South Island: 123 Plots. Common throughout the western side of the eastern South Island from the Wairau to the Rangitata River. Tends to be rare in the Canterbury foothills and is completely absent further east near the coast. It is also absent in the extreme west in the proximity of the Main Divide.

Southern South Island: 133 Plots. Common throughout the headwaters of the Waitaki and Clutha catchment from the Tasman River in the north to the Dart River in the South and also in the Eyre mountains. It is absent elsewhere in the southern South Island.

Fig. 14 - Association D 1, Waimakariri. Note the monotypic nature of the forest. Mountain beech is the only tree species. Shrub species are sparse and moss is often the only ground species.

Altitude: 2298-3808 feet. Sometimes forms the bushline but more generally gives way to other associations just short of bushline. The range of altitude in eastern South Island is from 2582-3926 feet. In southern South Island it is from 2091 to 3349 feet.

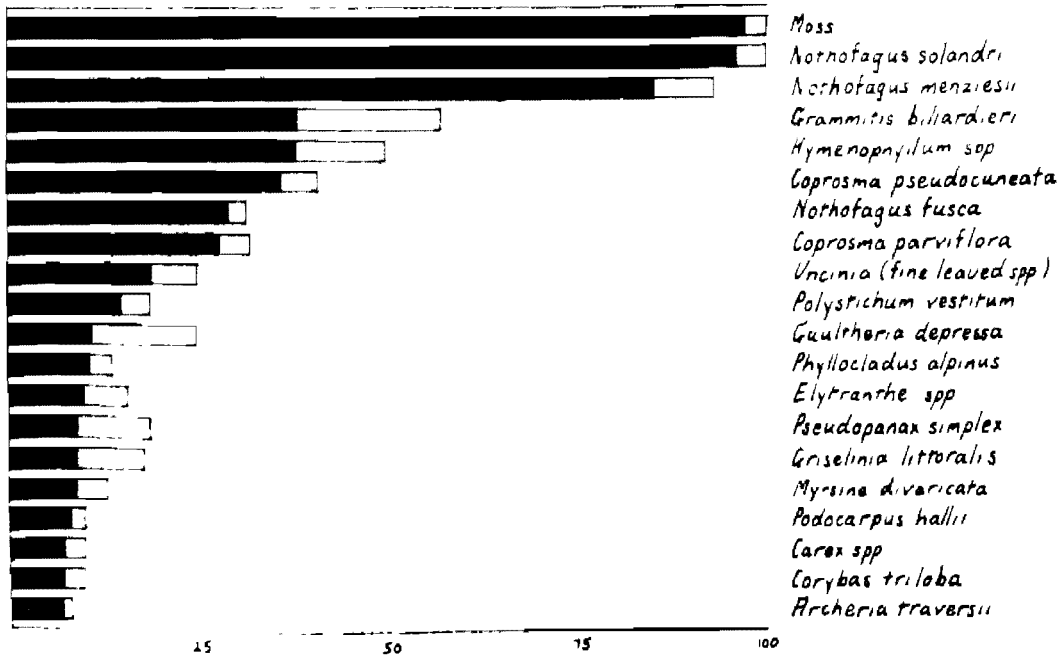
Physiography: Tends to be prevalent on moderately steep to steep faces and spurs.

Association D 2

No. of Plots: 272

Stand Structure and Composition

Community diagram:



Mean Complexity: 8.7 ± 0.3 ($P = 0.05$) species

Mean Stand Height: 50.3 ± 1.9 ($P = 0.05$) feet

Canopy Density: Dense

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Nothofagus menziesii.

Moderate Species: Nil.

Minor Species: Nothofagus fusca, Pseudopanax simplex, Griselinia littoralis, Podocarpus hallii.

Shrub Tiers: Open.

Major Species: Nil.

Moderate Species: Coprosma pseudocuneata.

Minor Species: Coprosma parviflora, Phyllocladus alpinus, Myrsine divaricata.

Ground Tiers: Open.

Major Species: Moss.

Moderate Species: Grammitis billardieri, Hymenophyllum spp.

Minor Species: Uncinia (fine leaved spp.), Polystichum vestitum, Gaultheria depressa, Corybas triloba, Carex spp.

Lianes, epiphytes, etc.:

Minor Species: Elytranthe spp.

Habitat

Area:

North Island: 11 Plots. Scattered throughout the range of mountain beech in the North Island but rare.

Northern and Western South Island: 87 Plots. A particularly important association in the headwaters of the Buller River and in the northern headwaters of the Grey River. Moderately important and in the Gordon Range, at the western end of the Richmond Range, and on the eastern side of the Tasman and Arthur Ranges. Absent in the west.

Eastern South Island: 62 Plots. Important close to the Main Divide from the Wairau southwards to the Poulter River. Does occur further south but is very rare.

Southern South Island: 112 Plots. Occurs in the ultimate headwaters of the Waitaki catchment. It is important in the head-

waters of the Clutha catchment and in the Eyre and Takitimu Mountain Ranges. It is quite important in eastern Fiordland from the Murchison Range south to the Hump Range, but was not recorded in western Fiordland.

Altitude: 2149-3703 feet. This association may reach bushline. In the northern and western South Island it has an altitudinal range of 2973 to 4067 feet. In the eastern South Island the range is from 2158 to 3466 feet whereas in the southern South Island the range is from 1819 to 3143 feet.

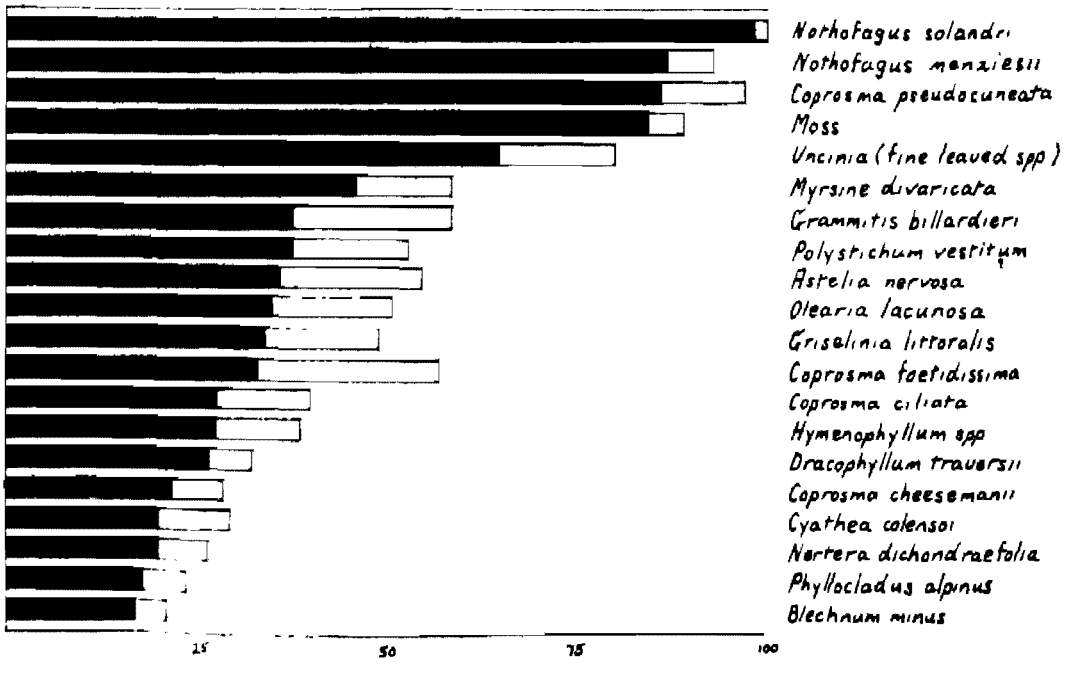
Physiography: Provided that there is adequate soil drainage it may occur on all sites though there is a slight tendency to occupy faces and spurs rather than gullies and terraces.

Association D 3

No. of Plots: 92

Stand Structure and Composition

Community diagram:



Mean Complexity: 16.8 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 41.0 $\pm$ 2.7 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech) Nothofagus menziesii.

Moderate Species: Griselinia littoralis.

Minor Species: Pseudopanax simplex, Nothofagus fusca.

Shrub Tiers: Moderate density.

Major Species: Coprosma pseudocuneata.

Moderate Species: Myrsine divaricata, Coprosma foetidissima, Olearia lacunosa.

Minor Species: Coprosma ciliata, Dracophyllum traversii, Phyllocladus alpinus, Hebe vernicosa, Pseudopanax colensoi, Pseudopanax lineare, Pittosporum (small leaved spp.), Senecio bennettii, Archeria traversii.

Ground Tiers: Moderate density.

Major Species: Moss, Uncinia (fine leaved spp.).

Moderate Species: Grammitis billardieri, Astelia nervosa, Polystichum vestitum, Hymenophyllum spp.

Minor Species: Nertera dichondraefolia, Coprosma cheesemanii, Cyathea colensoi, Gaultheria depressa, Blechnum minus, Chionochloa conspicua, Carex spp. Uncinia (large leaved spp.), Phormium colensoi, Blechnum fluviatile, Luzula spp., Myrsine nummularia.

Lianes, epiphytes, etc.:

Minor Species: Asplenium flaccidum.

Habitat

Area:

North Island: 0 Plots.

Northern and western South Island: 84 Plots. Important throughout the central region from the western Richmond Range and the Lead Hills in the north, through to the northern tributaries of the Grey River in the south.

Eastern South Island: 0 Plots.

Southern South Island: 8 Plots. Present throughout Fiordland but not common.

Altitude: 3077-4015 feet. Often forms a bushline.

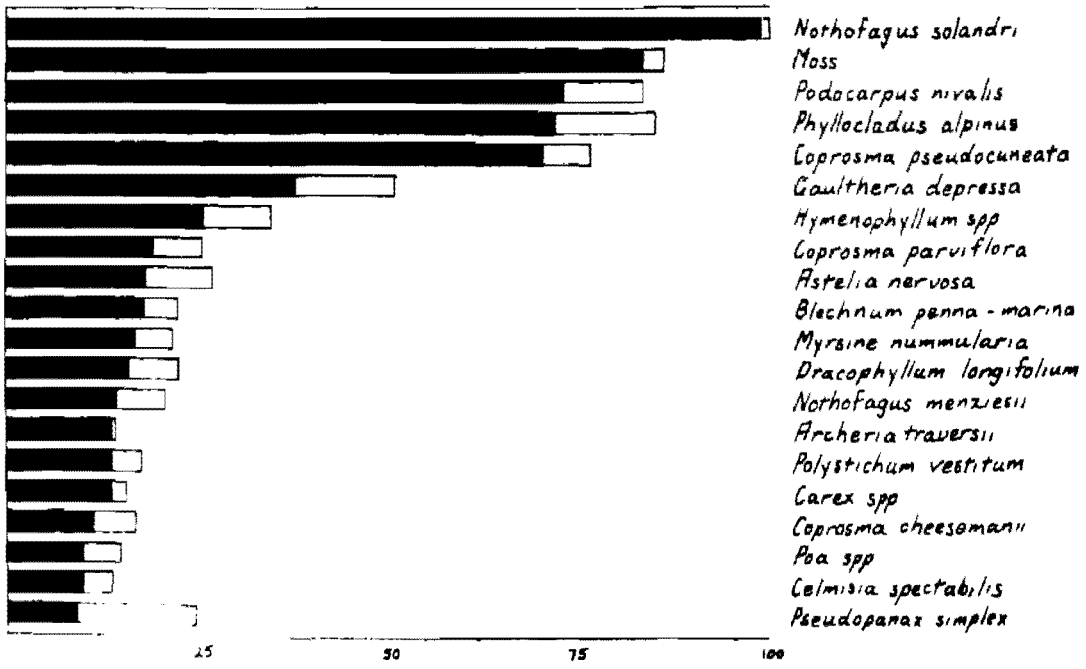
Physiography: Tends to occur mainly on the steeper slopes but shows no strong affinities to gully, face or spur sites.

Association D 4

No. of Plots: 111.

Stand Structure and Composition:

Community diagram:



Mean Complexity: 115 $\pm$ 0.8 (P = 0.05) species

Mean Stand Height: 30.6 $\pm$ 2.6 (P = 0.05)

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech).

Moderate Species: Nil.

Minor Species: Nothofagus menziesii.

Shrub Tiers: Moderate density.

Major Species: Phyllocladus alpinus, Podocarpus nivalis, Coprosma pseudocuneata.

Moderate Species: Nil.

Minor Species: Coprosma parviflora, Pseudopanax simplex, Dracophyllum longifolium, Archeria traversii, Pseudopanax colensoi, Dracophyllum uniflorum, Hebe vernicosa.

Ground Tiers: Open.

Major Species: Moss.

Moderate Species: Gaultheria depressa.

Minor Species: Hymenophyllum spp., Astelia nervosa, Myrsine nummularia, Polystichum vestitum, Coprosma cheesemanii, Carex spp., Poa spp., Celmisia spectabilis, Grammitis billardieri Lycopodium fastigiatum.

Habitat

Area:

North Island: 15 Plots. Restricted to the central regions in the vicinity of the Kaweka and Kaimanawa Ranges and Mt Ruapehu.

Northern and Western South Island: 23 Plots. Moderately important in the headwaters of the Buller catchment, but occasional stands do occur in the northern headwaters of the Grey River and on the eastern side of the Arthur Range.

Eastern South Island: 47 Plots. Particularly important in the Waimakariri and Rakaia catchments, but also occurs in the Hurunui and Waiau valleys and to a limited extent in the Canterbury foothills.

Southern South Island: 23 Plots. Quite important in the Waitaki and Clutha headwaters but occurs to a limited extent further south in the Eyre mountains and on the eastern side of Fiordland.

Altitude: 3173-4333 feet. This is an important bushline association. In the North Island it is more or less restricted to the bushline and the range is only 4021 to 4597 feet but in the eastern South Island and in the northern and western South Island it occupies a wider range of altitude. In the eastern South Island the range is from 3064 to 4146 feet and in the northern and western South Island the range is from 3720 to 4598 feet. In the southern South Island the range is more restricted again and is from 3111 to 3569 feet.

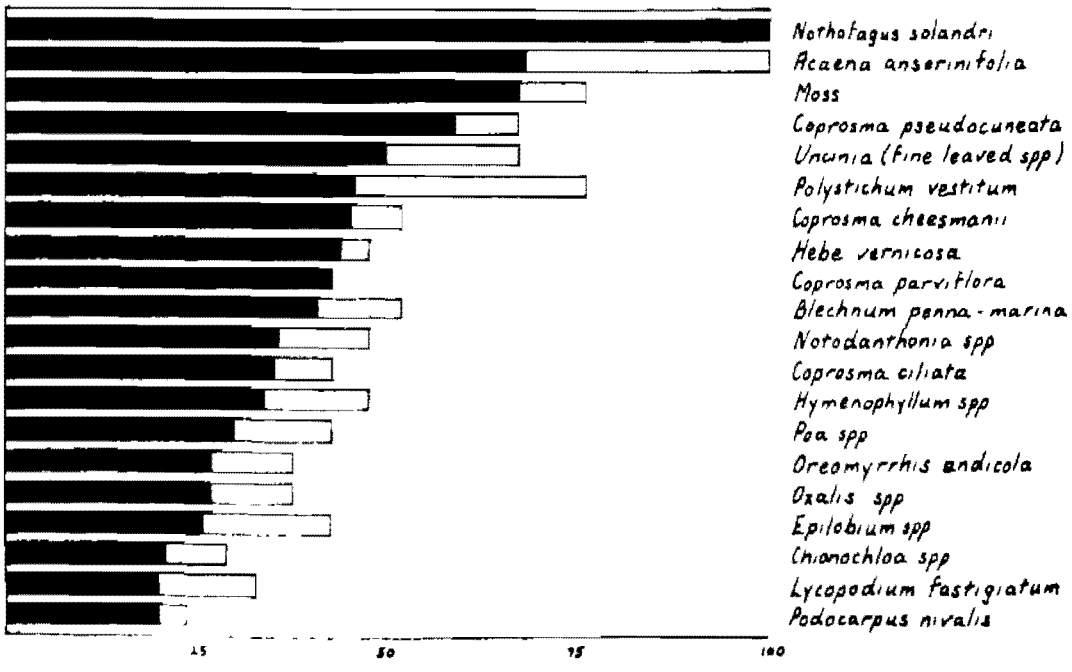
Physiography: Occurs mainly on moderately steep to steep faces and spurs.

Association E 1

No. of Plots: 21 (a minor association)

Stand Structure and Composition

Community diagram:



Mean Complexity: 21.6 ± 3.9 (P = 0.05) species

Mean Stand Height: 33.8 ± 6.4 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech).

Moderate Species: Nil.

Minor Species: Nil.

Shrub Tiers: Open.

Major Species: Nil.

Moderate Species: Coprosma pseudocuneata, Hebe vernicosa, Coprosma ciliata, Coprosma parviflora.

Minor Species: Podocarpus nivalis, Aristotelia fruticosa, Coprosma foetidissima, Pseudopanax simplex, Phyllocladus alpinus, Gaultheria antipoda, Hebe corriganii, Hebe odora, Pseudopanax colensoi.

Ground Tiers: Dense.

Major Species: Acaena anserinfolia, moss, Polystichum vestitum.

Moderate Species: Uncinia (fine leaved spp.), Blechnum penna-marina, Coprosma cheesemanii, Hymenophyllum spp., Notodanthonia spp., Epilobium spp., Poa spp.

Minor Species: Oreomyrrhis colensoi, Oxalis spp., Lycopodium fastigiatum, Chionochloa spp., Geranium microphyllum, Anisotome aromatica, Blechnum minus, Astelia nervosa, Carex spp., Celmisia spectabilis, Corybas triloba, Gaultheria depressa, Hypolepis millefolium, Myrsine nummularia, Ranunculus

hirtus, Helichrysum filicaule, Lagenophora pumila, Lagenophora petiolata, Blechnum fluviatile, Forstera bidwillii, Luzula spp., Gurisia macrophylla, Ranunculus lappaceus, Taraxacum spp., Viola filicaulis, Cotula spp.

Habitat

Area:

North Island: 6 Plots. Occasional in the southern Kaweka and northern Ruahine Ranges.

Northern and Western South Island: 7 Plots. Rare and scattered throughout the eastern side from the Grey River to the Richmond Range.

Eastern South Island: 7 Plots. Rare and scattered throughout the western side close to the Main Divide.

Southern South Island: 1 Plot from the Waitaki headwaters.

Altitude: 3698-4518 feet. Nearly always close to bushline.

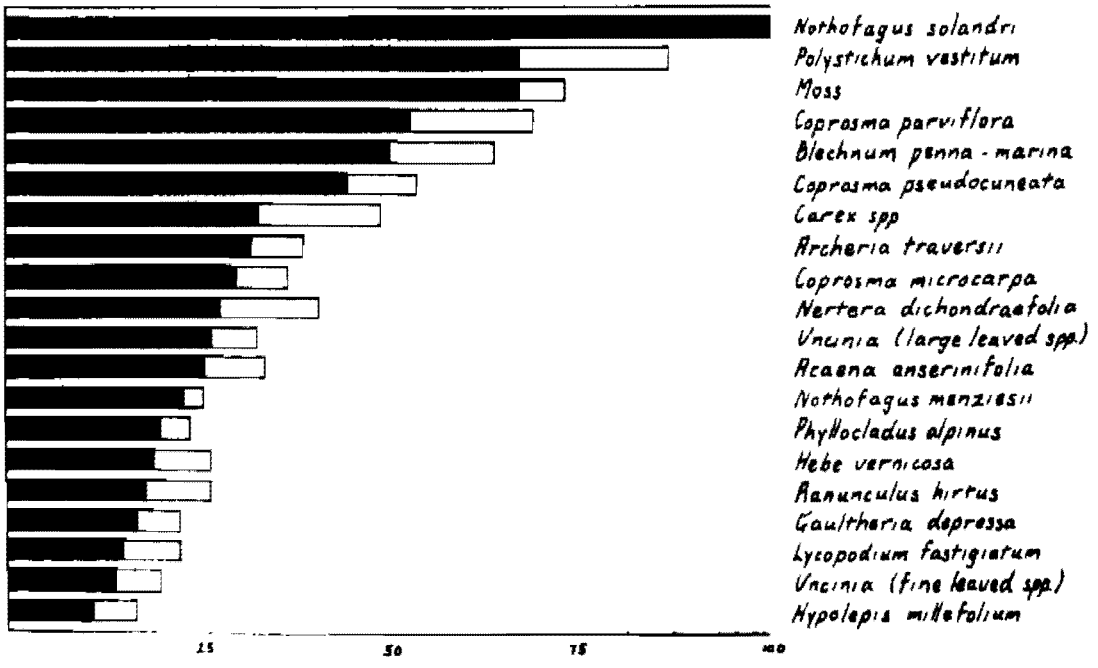
Physiography: Generally tends to occupy the steeper slopes.

Association E 2

No. of Plots: 70

Stand Structure and Composition

Community diagram:



Mean Complexity: 12.5 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 46.4 $\pm$ 3.2 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech).

Moderate Species: Nil.

Minor Species: Nothofagus menziesii.

Shrub Tiers: Moderate density.

Major Species: Nil.

Moderate Species: Coprosma parviflora,

Coprosma pseudocuneata.

Minor Species: Archeria traversii, Coprosma microcarpa, Hebe vernicosa, Phyllocladus alpinus, Aristotelia fruticosa, Coprosma linariifolia.

Ground Tiers: Moderate density.

Major Species: Polystichum vestitum, moss.

Moderate Species: Blechnum penna-marina, Carex spp., Nertera dichondraefolia.

Minor Species: Acaena anserinifolia, Uncinia (large leaved spp.), Ranunculus hirtus, Gaultheria depressa, Lycopodium fastigiatum, Uncinia (fine leaved spp.), Hypolepis millefolium, Senecio lagopus, Grammitis billardieri, Histopteris incisa, Poa spp., Astelia nervosa.

Habitat

Area:

North Island: 2 Plots, both located centrally and both of marginal affinities.

Northern and Western South Island: 2 Plots, both in the Buller headwaters.

Eastern South Island: 66 Plots. Important in the Waiau and Wairau catchments, but also occurs southwards as far as the Rakaia River, and is occasionally present in the Canterbury foothills.

Southern South Island: Nil.

Altitude: 2784-3960 feet.

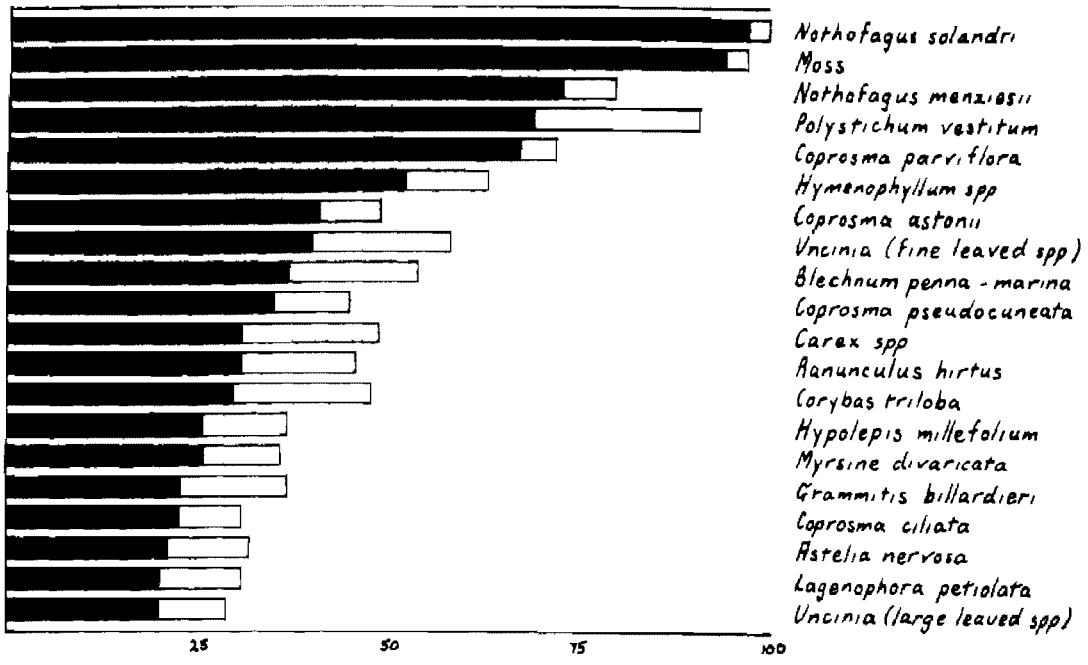
Physiography: Fairly variable. Tends to be restricted to steeper slopes.

Association E 3

No. of Plots: 120

Stand Structure and Composition

Community diagram:



Mean Complexity: 17.1 $\pm$ 0.9 (P = 0.05) species

Mean Stand Height: 55.7 $\pm$ 2.7 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Nothofagus menziesii.

Moderate Species: Nil.

Minor Species: Pseudopanax colensoi, Nothofagus fusca, Pseudopanax crassifolium, Griselinia littoralis, Pseudopanax simplex.

Shrub Tiers: Moderate density.

Major Species: Coprosma parviflora.

Moderate Species: Coprosma astonii, Coprosma pseudocuneata.

Minor Species: Myrsine divaricata, Coprosma ciliata, Coprosma rhamnoides, Coprosma linarifolia, Podocarpus nivalis.

Ground Tiers: Moderate density.

Major Species: Moss, Polystichum vestitum.

Moderate Species: Hymenophyllum spp., Uncinia (fine leaved spp.), Blechnum penna-marina, Carex spp., Corybas triloba, Ranunculus hirtus.

Minor Species: Hypolepis millefolium, Grammitis billardieri, Astelia nervosa, Lagenophora petiolata, Uncinia (large leaved spp.), Viola filicaulis, Cardamine debilis, Nertera dichondraefolia, Coprosma cheesemanii, Acaena anserinifolia, Blechnum fluviatile, Epilobium spp.

Lianes, epiphytes, etc.:

Minor Species: Rubus cissoides, Elytranthe spp.

Habitat

Area:

North Island: Nil.

Northern and Western South Island: 7 Plots. Rare but scattered throughout the eastern side from the Grey headwaters northwards.

Eastern South Island: 12 Plots. Scattered stands occur from the Rangitata northwards to the Waiau.

Southern South Island: 101 Plots. Particularly important in the Eyre mountains, but does extend into the Takitimu Range and the Hunter Range of eastern Fiordland. It is also quite important further north in the headwaters of the Clutha and Waitaki catchments.

Altitude: 1856-3196 feet. Sometimes occurs at bushline.

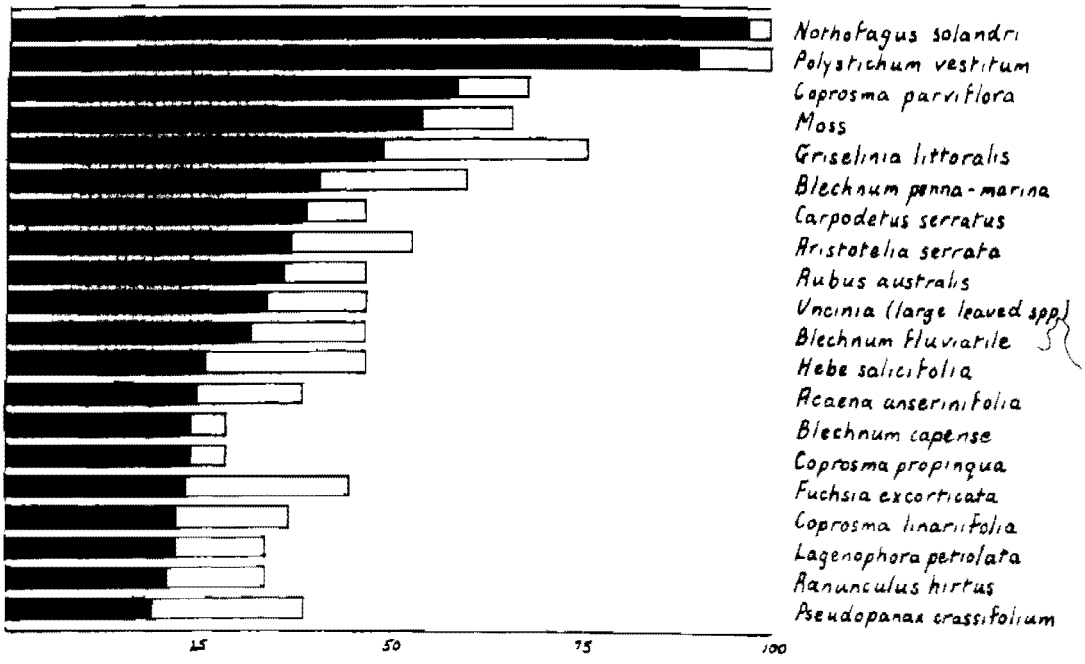
Physiography: Tends to occupy gentle sloping gullies and terrace sites but may be important elsewhere.

Association E 4

No. of Plots: 38 (a minor association)

Stand Structure and Composition:

Community diagram:



Mean Complexity: 19.3 $\pm$ 1.4 (P = 0.05) species

Mean Stand Height: 54.5 $\pm$ 3.1 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech), Griselinia littoralis.

Moderate Species: Aristotelia serrata, Carpodetus serratus, Fuchsia excorticata.

Minor Species: Pseudopanax crassifolium, Podocarpus hallii, Nothofagus fusca, Pseudopanax simplex, Nothofagus menziesii, Hoheria lyallii.

Shrub Tiers: Moderate density.

Major Species: Nil.

Moderate Species: Coprosma parviflora, Hebe salicifolia.

Minor Species: Coprosma linariifolia, Coprosma propinqua, Coprosma rhamnoides, Pittosporum tenuifolium, Coprosma colensoi, Aristotelia fruticosa, Olearia arborescens, Coprosma lucida, Coprosma ciliata.

Ground Tiers: Dense.

Major Species: Polystichum vestitum.

Moderate Species: Moss, Blechnum penna-marina, Blechnum fluviatile, Uncinia (large leaved spp.).

Minor Species: Acaena anserinifolia, Lagenophora petiolata, Ranunculus hirtus, Blechnum capense, Grammitis billardieri, Corybas triloba, Carex spp., Epilobium spp., Erechtites spp., Helichrysum bellidioides, Cardamine debilis, Uncinia (large leaved spp.), Hypolepis millefolium, Celmisia spectabilis, Asplenium hookerianum, Astelia nervosa, Blechnum minus, Nertera depressa, Poa spp.

Lianes, epiphytes, etc.:

Moderate Species: Rubus australis.

Minor Species: Rubus cissoides, Elytranthe spp., Muehlenbeckia complexa.

Habitat

Area:

North Island: 0 Plots.

Northern and Western South Island: 0 Plots.

Eastern South Island: 16 Plots. Mostly in the south, in the Rangitata and Rakaia catchments.

Southern South Island: 22 Plots. Moderately important in the headwaters of the Clutha and Waitaki catchments.

Altitude: 1563-2541 feet. In the eastern South Island the range is 1777-2813 feet. In the southern South Island the range is 1496-2254 feet.

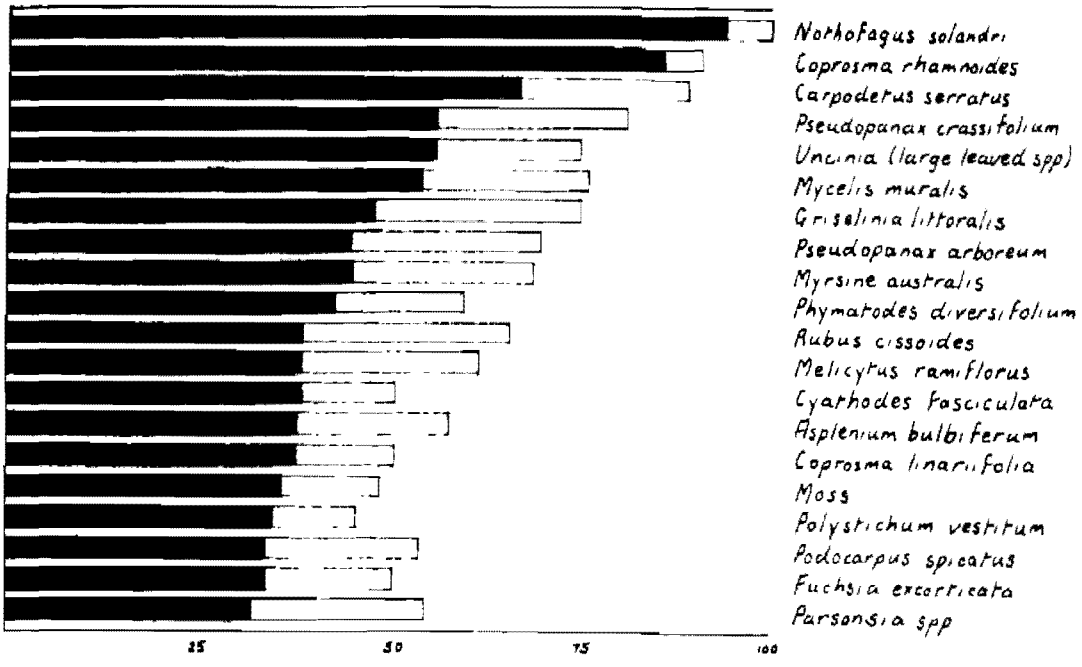
Physiography: Generally occupies gullies and terraces.

Association F 1

No. of Plots: 93

Stand Structure and Composition

Community diagram:



Mean Complexity: 30.0 ± 1.5 (P = 0.05) species

Mean Stand Height: 62.0 ± 3.0 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (black beech or mountain beech), Carpodetus serratus, Pseudopanax crassifolium, Griselinia littoralis, Pseudopanax arboreum.

Moderate Species: Myrsine australis, Melicytus ramiflorus, Podocarpus spicatus, Fuchsia excorticata, Coprosma linariifolia, Pittosporum tenuifolium.

Minor Species: Leptospermum ericoides, Podocarpus hallii, Aristotelia serrata, Pittosporum eugenioides, Sophora microphylla, Elaeocarpus hookerianus, Pennantia corymbosa, Nothofagus fusca, Elaeocarpus dentatus, Podocarpus ferrugineus, Podocarpus totara, Dacrydium cupressinum.

Shrub Tiers: Dense.

Major Species: Coprosma rhamnoides.

Moderate Species: Cyathodes fasciculata.

Minor Species: Coprosma robusta, Pseudowintera colorata, Helichrysum glomeratum, Coprosma parviflora, Coprosma lucida, Coprosma australis, Cyathea dealbata, Cyathodes juniperina, Olearia paniculata, Coprosma microcarpa, Coprosma crassifolia, Hebe traversii, Hedycarya arborea, Coprosma rotundifolia, Coprosma propinqua, Schefflera digitata.

Ground Tiers: Dense.

Major Species: Mycelis muralis, Uncinia (large leaved spp.).

Moderate Species: Phymatodes diversifolium, Asplenium bulbiferum, moss, Polystichum vestitum, Uncinia (fine leaved spp.).

Minor Species: Polystichum richardii, Microlaena avenacea, Blechnum minus, Blechnum discolor, Blechnum fluviatile, Ranunculus hirtus, Blechnum lanceolatum, Carex spp., Cardamine debilis, Astelia nervosa, Libertia ixioides, Blechnum capense, Hydrocotyle spp., Hypochoeris radicata, Pteridium aquilinum, Corybas triloba, Hypolepis millefilium, Pterostylis spp.

Lianes, epiphytes, etc.:

Moderate Species: Rubus cissoides, Parsonsia

spp., Asplenium flaccidum.

Minor Species: Clematis spp., Clematis paniculata, Rhipogonum scandens, Metrosideros diffusa, Muehlenbeckia complexa, Pyrrosia serpens.

Habitat

Area:

North Island: 3 Plots, one in the northern Ruahine Range and two in the Aorangi Range.

Northern and Western South Island: 7 Plots. Chiefly in the vicinity of the Motueka River and the Gordon Range, though occasional stands do occur further to the north and west in the vicinity of the Aorere River.

Eastern South Island: 83 Plots. A very important association in the Seaward Kaikoura Range. Occasional stands occur further south along the coast at Motunau and the association also occurs near the southern extremities of the Canterbury foothills, from Mt Hutt to the Waihi River.

Southern South Island: 0 Plots.

Altitude: 638-1932 feet.

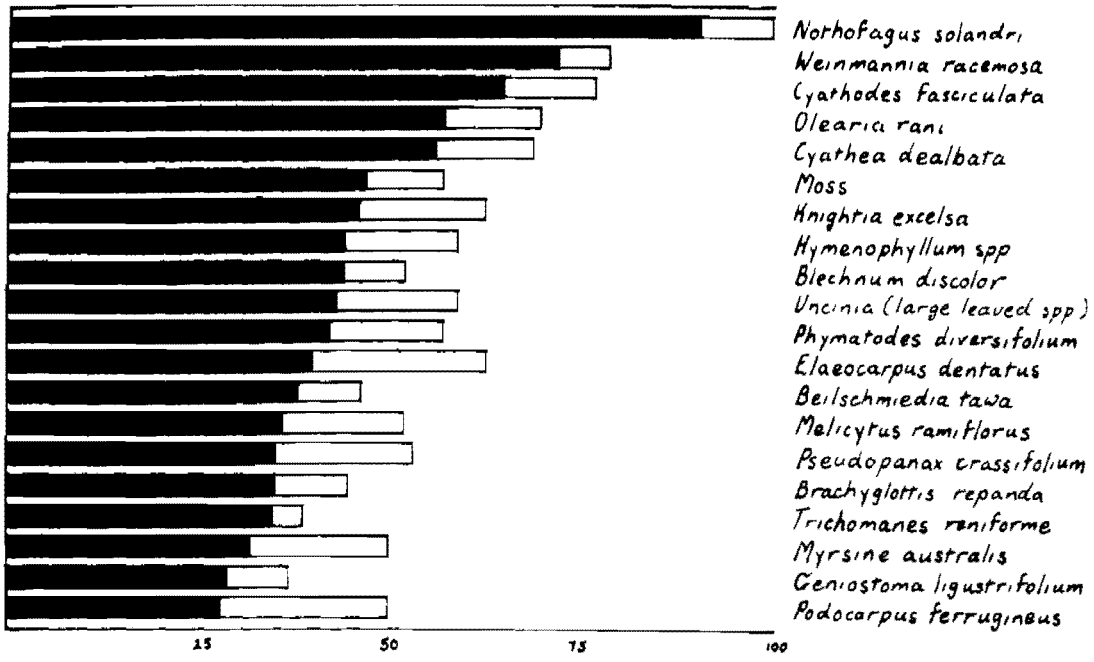
Physiography: Shows a tendency to occur more often on terraces and gullies than elsewhere.

Association F 2

No. of Plots: 126

Stand Structure and Composition

Community diagram:



Mean Complexity: 26.2 $\pm$ 1.2 (P = 0.05) species

Mean Stand Height: 65.4 $\pm$ 2.8 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (black beech, rarely mountain beech), Weinmannia racemosa, Olearia rani.

Moderate Species: Knightia excelsa, Elaeocarpus dentatus, Pseudopanax crassifolium, Melicytus ramiflorus, Podocarpus ferrugineous, Myrsine australis, Beilschmiedia tawa.

Minor Species: Pseudopanax arboreum, Dacrydium cupressinum, Carpodetus serratus, Podocarpus hallii,

Nothofagus truncata, Metrosideros robusta, Griselinia littoralis, Gymnelaea lanceolata, Cyathea medullaris, Nothofagus fusca, Coprosma linariifolia, Leptospermum ericoides.

Fig. 15 - Association F 1, Wanganui. A low altitude black beech association which is usually restricted to spurs. Note the ground cover of large leaved Uncinia spp.

Shrub Tiers: Dense.

Major Species: Cyathodes fasculata.

Moderate Species: Cyathea dealbata, Brachyglottis repanda, Hedycarya arborea.

Minor Species: Geniostoma ligustrifolium, Coprosma rhamnoides, Coprosma australis, Coprosma robusta, Coprosma lucida, Cyathodes juniperina, Cyathea smithii, Dicksonia squarrosa, Pseudowintera axillaris, Coprosma tenuifolia.

Ground Tiers: Dense.

Major Species: Nil.

Moderate Species: Uncinia (large leaved spp.), Hymenophyllum spp., Phymatodes diversifolium, moss, Blechnum discolor, Astelia nervosa.

Minor Species: Trichomanes reniforme, Microlaena avenacea, Blechnum capense, Asplenium bulbiferum, Freycinetia banksii, Grammitis billardieri, Asplenium falcatum, Dianella intermedia, Blechnum lanceolatum, Polystichum richardii, Gahnia procera, Pteridium aquilinium, Blechnum fluviatile, Asplenium lucidum, Todea hymenophylloides, Uncinia (fine leaved spp.).

Lianes, epiphytes, etc.:

Minor Species: Asplenium flaccidum, Rhipogonum scandens, Metrosideros diffusa, Parsonsia spp.

Habitat

Area:

North Island: 101 Plots. With the exception of the central areas, in the vicinity of the southern Kaweka and the Kaimanawa Ranges, this is an important association throughout the range of Nothofagus solandri in the North Island. It is particularly important in the Wanganui area and to the north.

Northern and Western South Island: 21 Plots. Quite important in the north in the vicinity of the Pelorus Sounds and in the lower Motueka, Takaka and Aorere river catchments.

Eastern South Island: 4 Plots. Occasional near the coast in the Seaward Kaikoura Range.

Southern South Island: 0 Plots.

Altitude: 426-1492 feet. In the North Island the range is from 540 to 1586 feet. In the northern and western South Island the range is from 204 to 876 feet.

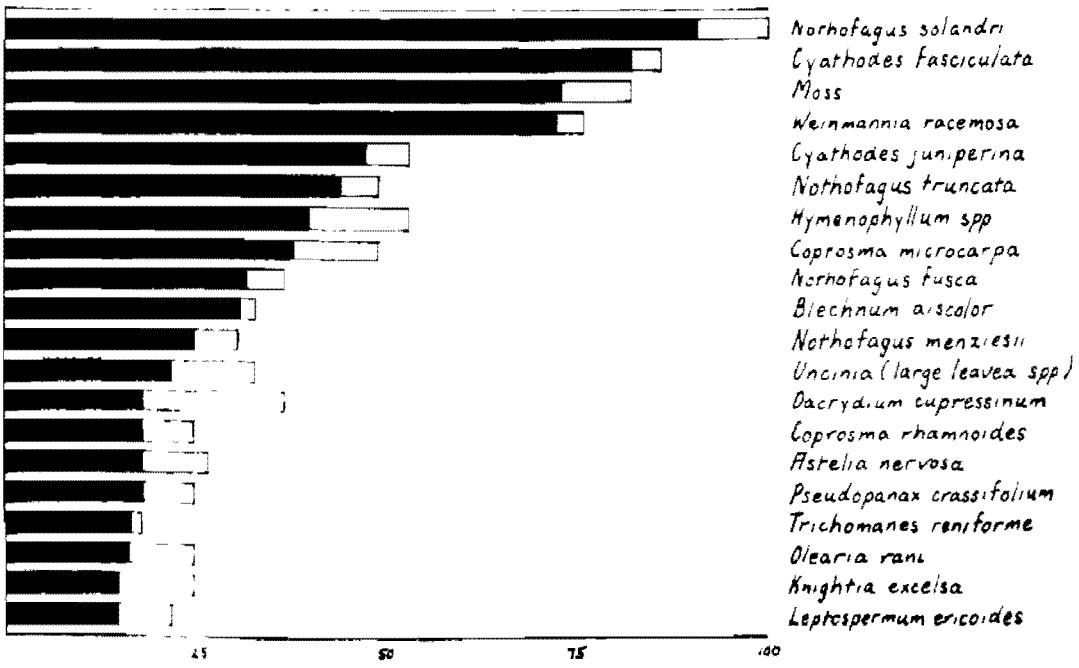
Physiography: Largely restricted to spurs and terraces.

Association F 3

No. of Plots: 51

Stand Structure and Composition

Community diagram:



Mean Complexity: 14.8 $\pm$ 1.5 (P = 0.05) species

Mean Stand Height: 53.3 $\pm$ 4.2 (P = 0.05) feet

Canopy Density: Variable

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (black beech, occasionally mountain beech), Weinmannia racemosa.

Moderate Species: Nothofagus truncata.

Minor Species: Dacrydium cupressinum, Nothofagus fusca, Podocarpus ferrugineus, Nothofagus menziesii, Knightia excelsa, Pseudopanax crassifolium, Olearia rani, Leptospermum ericoides, Carpodetus serratus, Pseudopanax arboreum, Podocarpus hallii, Elaeocarpus hookerianus, Myrsine salicina, Elaeocarpus dentatus, Metrosideros robusta, Pittosporum tenuifolium.

Shrub Tiers: Moderate density.

Major Species: Cyathodes fasciculata.

Moderate Species: Cyathodes juniperina, Coprosma microcarpa.

Minor Species: Coprosma rhamnoides, Coprosma foetidissima, Cyathea dealbata, Geniostoma ligustrifolium, Hedycarya arborea.

Ground Tiers: Moderate density.

Major Species: Moss.

Moderate Species: Hymenophyllum spp.

Minor Species: Blechnum discolor, Uncinia (large leaved spp.), Astelia nervosa, Grammitis billardieri, Trichomanes reniforme, Phymatodes diversifolium, Carex spp.

Lianes, epiphytes, etc.:

Minor Species: Asplenium flaccidum.

Habitat

Area:

North Island: 46 Plots. Important in the south, i.e. in the Aorangi, Rimutaka, Tararua and southern Ruahine Ranges. Rare in

the Huiarau Range and Wanganui areas.

Northern and Western South Island: 5 Plots. Rare and scattered in the vicinity of the Marlborough Sounds and the Pelorus catchment.

Eastern South Island: 0 Plots.

Southern South Island: 0 Plots.

Altitude: 674-1926 feet.

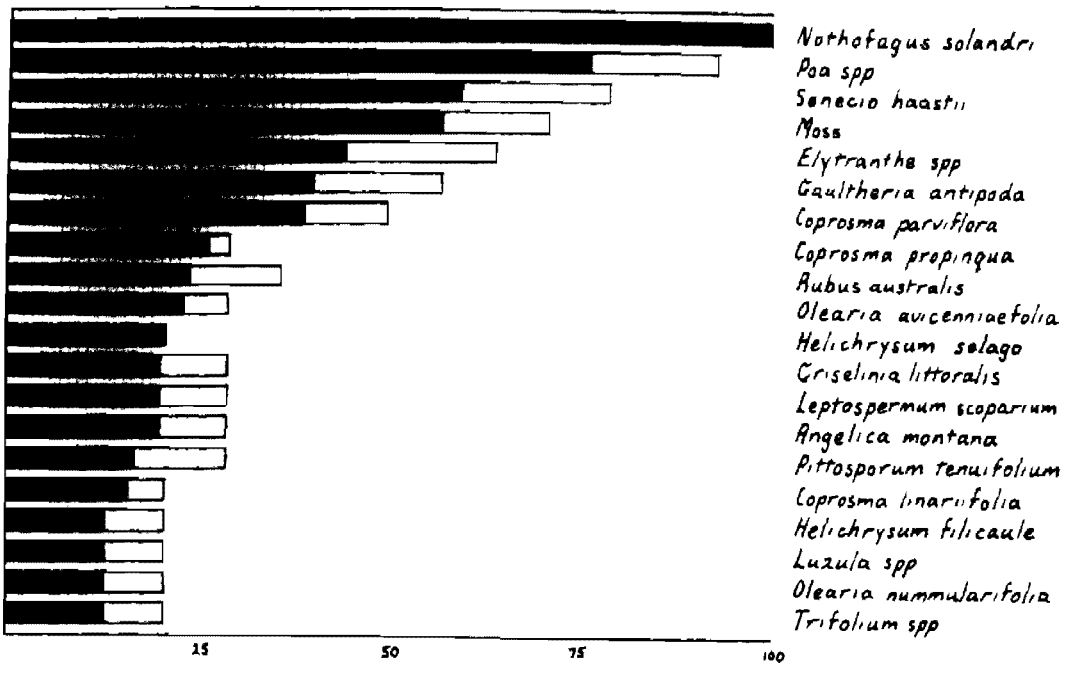
Physiography: largely restricted to spurs and steeply eroding gullies.

Association G 1

No. of Plots: 14 (a minor association)

Stand Structure and Composition

Community diagram:



Mean Complexity: 13.8 $\pm$ 2.4 (P = 0.05) species

Mean Stand Height: 30.6 $\pm$ 8.2 (P = 0.05) feet

Canopy Density: Open

Tier Composition:

Tree Tiers: Major Species: Nothofagus solandri (mountain beech).

Moderate Species: Nil.

Minor Species: Griselinia littoralis, Pittosporum tenuifolium.

Shrub Tiers: Open.

Major Species: Nil.

Moderate Species: Gaultheria antipoda, Coprosma parviflora.

Minor Species: Coprosma propinqua, Leptospermum scoparium, Olearia avicenniaefolia, Coprosma linariifolia, Olearia nummularifolia, Hebe salicifolia, Carpodetus serratus, Coprosma virescens, Cyathodes juniperina, Helichrysum glomeratum, Phyllocladus alpinus.

Ground Tiers: Moderate density.

Major Species: Poa spp., Senecio haastii, Moss.

Moderate Species: Nil.

Minor Species: Angelica montana, Helichrysum filicaule, Luzula spp., Trifolium spp., Helichrysum selago, Carmichaelia petriei, Asplenium hookerianum, Asplenium richardii, Blechnum penna-marina, Cardamine debilis, Cyathodes fraseri, Hypochaeris radicata, Notodanthonia spp., Uncinia (fine leaved spp.), Coriaria sarmentosa, Pteridium aquilinum, Festuca novae-zelandiae.

Lianes, epiphytes, etc.:

Moderate Species: Elytranthe spp.

Minor Species: Rubus australis.

Habitat

Area:

North Island: 0 Plots.

Northern and Western South Island: 0 Plots.

Eastern South Island: 1 Plot from the mid Clarence valley.

Southern South Island: 13 Plots. Except for one stand from the Waitaki headwaters, this association was only observed from the southern end of Lake Hawea.

Altitude: 1603-2709 feet.

Physiography: Insufficient plots located in this association to indicate trend.

3.4. SUMMARY AND CONCLUSIONS

It has been mentioned in the introduction to this section that the purpose of the division of Nothofagus solandri forest and scrub-land into a number of plant associations is to provide a basis to study the variation in behaviour of Nothofagus solandri throughout its range of habitat, and to throw some light on the properties which allow it to exist and to compete with other species on certain sites.

The breakdown can thus be considered to have been successful if:

(a) the numerical system involving the use of indices of similarity and cluster analysis did in fact satisfactorily subdivide on the basis of the plant species or other taxa which were used for the analysis

(b) the associations so formed produced a satisfactory subdivision

of the site factors affecting the growth and ecological behaviour of Nothofagus solandri,

(c) each association represented a reasonably uniform unit in terms of plant composition, stand structure and site.

To test the first of these requirements in absolute terms would require employment of other lengthy methods of classification for comparison purposes and even if such comparisons were employed there would be difficulty in interpretation. That this requirement is in fact satisfied is apparent on examination of the preceding descriptions of the associations. There is little doubt that the numerical system has worked and worked satisfactorily. If it had not worked at all, it would be expected that each species would be more or less spread regularly throughout all associations. Table 1 demonstrates that this is far from the case. In Table 1 the five most important species other than Nothofagus solandri have been taken from each of the 23 associations (that is ignoring those species groups, such as Uncinia fine leaved spp., which could not be reduced to specific level). The percent frequency of each of the 46 species thus selected has been given for each of the associations. It can be seen that only three species are represented in all of the 23 associations. These are Griselinia littoralis, Nothofagus menziesii and Podocarpus hallii, but even these particularly wide ranging species are by no means regularly distributed i.e. Griselinia littoralis has a range from 6 percent frequency in Associations A 1 and F 3 through to 92 percent in C 1. Nothofagus menziesii ranges from 3 percent frequency in Association F 1 through to 93 percent in Associations D 2 and D 3. Podocarpus hallii ranges from 3 percent frequency in Association F 2

Table 2 - Habitat of the 23 associations. Crosses indicate the conditions of Locality, Rainfall, Altitude, Drainage, Soil Development and Canopy Density for each Association

Association	Locality				Rainfall			Altitude			Drainage			Soil Development			Canopy	
	N & W		E	S														
	N.I.	S.I.	S.I.	S.I.	High	Mod	Low	High	Med	Low	Good	Mod	Poor	Deep	Mod	Shallow	Open	Dense
A 1	x	x		x	x			x	x		x	x	x			x	x	
B 1		x		x	x			x	x		x				x	x	x	x
B 2	x	x			x				x	x			x	x	x		x	
B 3		x		x	x	x				x		x	x	x				x
B 4		x		x	x					x		x	x		x	x	x	
C 1		x	x				x		x		x				x		x	x
C 2	x				x	x			x	x		x	x	x			x	
C 3	x		x			x	x		x	x	x			x			x	x
C 4	x	x					x		x		x			x	x		x	x
C 5	x		x	x		x			x		x			x				x
C 6	x					x		x	x		x			x	x		x	x
D 1			x	x			x	x	x		x			x	x			x
D 2		x	x	x		x		x	x		x			x				x
D 3		x				x		x			x			x	x		x	
D 4	x	x	x	x		x	x	x			x			x	x		x	
E 1	x	x	x			x	x	x			x			x	x		x	
E 2			x			x		x	x		x			x	x		x	
E 3				x		x		x	x		x			x			x	x
E 4			x	x		x	x		x		x			x	x		x	
F 1			x				x			x	x				x		x	
F 2	x	x				x	x			x	x				x		x	x
F 3	x						x			x	x				x		x	x
G 1				x			x		x		x			x	x		x	

through to 87 percent frequency in Association C 2. Weinmannia racemosa is an example of a species with a more restricted range. It has 100 percent frequency in Association B 4 and has a high percent frequency in Association F 2, F 3, B 1 and B 3 but it has a low percent frequency in Associations C 2, C 4, B 2, C 5, A 1, C 3, C 1 and F 1 and is absent from the remaining ten associations.

The 23 associations, as far as can be assessed do represent different environmental niches. However it is hard to define the habitat of each in absolute terms. For instance there must be factors which are unable to be identified at present which have a strong influence on the behaviour of Nothofagus solandri and other plant species. Interactions must occur between even the most apparent and most easily measurable factors and most of the attributes which can be recognised and measured, such as altitude, locality, and canopy density are not in fact single elements of the environment, but rather they represent combinations of a number of elements such as length of growing season, temperature, rainfall, light, humidity, etc. each of which is important in helping to determine plant growth. Nevertheless it is apparent that each association has a certain restricted range of locality, altitude, rainfall*, soil drainage, soil development and canopy density, over which it occurs (see Table 2). For instance, none of the associations occur at both high and low altitude, only 5 out of the 23 associations are import-

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* Estimates of high (150 inch annual +), medium (80-150 inches) and low (less than 80 inches) rainfall have been based on provisional isohyet maps produced by the Meteorological Dept. These maps are often inaccurate especially in the regions where much of this study was undertaken.

ant in more than 2 of the 4 defined localities, none of the associations which occupy areas of deep soil development also occupy areas of shallow soil development and there is only one association which may grow in areas of both good and poor soil drainage. Thus even though it is probably impossible to define the habitat of each association in absolute terms, it is possible to give a generalised account of the type of habitat that each occupies. For instance, from Table 2 it is apparent that Association A 1 occurs in high rainfall areas, mainly on the western side of the country. It is restricted to the upper forest and scrub belts, to areas where depth of soil development is poor and where soil drainage may also be poor. In contrast, Association F 3 is more or less restricted to low altitude, low rainfall areas in the North Island where drainage is good and soil development is moderate.

It appears that the numerical classification system has satisfactorily subdivided the Nothofagus solandri forest and scrubland into associations, and that these associations each represent a certain and different environmental niche. It remains to demonstrate that the subdivision is a meaningful one in terms of the growth and behaviour of Nothofagus solandri and in the structure of the Nothofagus solandri associations. The variation in the behaviour of Nothofagus solandri between the associations is discussed in the next section. It is sufficient here to highlight, by examples, how the structure may vary. To do this two examples, complexity and stand height have been used.

The mean complexity of associations with respect to vascular species (plus "moss") varies from 5.2 ± 0.3 ($P = 0.05$) species in

Associations D 1 through to 30.0 $\pm$ 1.5 (P = 0.05) species in Association F 1. The complexity is highest in the low altitude associations B 3, C 2, F 1 and F 2 and lowest in the low rainfall, moderately high altitude associations D 1, D 2, D 4 and C 1, all of which tend to have dense canopies. There tends to be a high complexity in some of the associations which occur on sites marginal for the survival of Nothofagus solandri. For instance there is little difference in the mean complexity of Associations F 2, A 1 and E 1, and whereas Association F 2 occurs at low altitudes on sites of moderate to low rainfall with good drainage and moderately deep soil development and is thus quite a reasonable site for growth, Association A 1 occurs at fairly high altitudes where soil development is poor and soil drainage may be poor and E 1 occurs near bushline where rainfall tends to be low. The mean complexity of F 2 is 26.2 $\pm$ 1.2 (P = 0.05) species. That of A 1 is 23.4 $\pm$ 1.8 (P = 0.05) species and that of E 1 is 21.6 $\pm$ 3.9 (P = 0.05) species. However, even though the overall complexity of species composition is similar in all three, the number of genera represented in A 1 and E 1 tends to be lower than in F 2 and whereas two-thirds of the species which have percentage frequencies greater than 40 percent in F 2 and A 1 are tree or shrub species and only one-third are ground species, the reverse is the case in Association E 1, i.e. two-thirds of the species are ground species.

The mean stand height varies from 17.4 $\pm$ 3.4 (P = 0.05) feet in association A 1 to 66.5 $\pm$ 4.1 (P = 0.05) feet in Association C 2. The tallest associations are those which occur at low to mid altitudes i.e. C 2, C 4, C 5, F 1 and F 2. There is a reduction in the mean

stand height with gain in altitude, with deterioration in drainage, with deterioration in soil development and as the rainfall becomes marginally low for Nothofagus solandri. For instance, in the five low altitude associations above, the mean stand height in each case exceeds 60 feet. In Associations D 3, D 4 and E 1, which are restricted to high altitudes, the mean stand height for each is between 30 and 41 feet. In Association B 2 which occurs in areas where soil drainage is poorest, the mean stand height is 37.3 feet and in Association A 1 which occupies sites of poor soil development the mean stand height is only 17.4 feet.

In a preceding paragraph the problem of interaction of environmental factors or factor complexes to define the habitat niche of a particular association, or for that matter of a particular species, has been mentioned. The interaction between altitude and area provides a good example to demonstrate the magnitude of the influence such interactions can have, and at the same time it provides a good example of why site has been classified in terms of the end product - i.e. the vegetation growing on the site, rather than on the primary physical and climatic site factors. Associations B 2, C 4, C 5 and D 4 are all important in both the North Island and in the northern and western South Island. In each case, however, the associations occupy a higher altitudinal belt in the North Island. The mean altitudes of the associations in the North Island are, respectively, 1300 feet, 700 feet, 700 feet and 200 feet higher than in the northern and western South Island. The difference is greatest in the association which occupies the lower altitude wetter sites and least in the association which occupies high altitude drier sites.

Associations C 5, D 2 and D 4 are important in both the northern and western South Island and in the eastern South Island. The mean altitude of the associations in the northern and western South Island are respectively 300 feet, 700 feet and 500 feet higher than in the eastern South Island. Associations C 5, D 1, D 2 and D 4 are important both in the eastern South Island and in the southern South Island. The mean altitude of the associations in the eastern South Island are respectively 700 feet, 600 feet, 300 feet and 300 feet higher than in the southern South Island. It can be seen that the mean altitude of the associations of Nothofagus solandri are, on the average, some 1700 feet lower in the southern South Island than in the North Island. This particular interaction has an important bearing when considering the absence of black beech in the southern South Island. The two main black beech associations, F 2 and F 3 are largely restricted to the North Island. Association F 1 occupies a belt in the North Island of 540 to 1586 feet (1 standard deviation around the mean). Association F 2 occupies a belt in the North Island of 674 to 1926 feet.

To understand the role played by Nothofagus solandri in any particular plant community requires some understanding of the requirements and tolerances of the other species as well as Nothofagus solandri. By comparison of Table 1 with Table 2 it is possible to begin to elucidate the ecological tolerances of the 46 species listed in Table 1, in terms of plant competition, soil drainage, soil development, altitude and rainfall, within the Nothofagus solandri communities. For instance, we can see from Table 1 that Olearia colensoi has a high percent frequency of occurrence only in the

association which occurs at moderate to high altitudes, in high rainfall areas, where the rock is erosion resistant and soil development is poor. Elsewhere it is absent or has a low percent frequency. It would follow that Olearia colensoi has a poor competitive ability. on the better sites for forest growth, that it has a poor tolerance for low rainfall conditions, but has a strong tolerance for conditions at high altitudes and shallow soil development where the rainfall is high. On the other hand, Olearia rani has a high percent frequency at low altitudes where rainfall is moderate to low, where drainage is good and soil development moderate. It can be assumed therefore that it has a reasonable ability to compete and a reasonable tolerance for low rainfall conditions, but poor tolerance for conditions of high altitude and high soil moisture.

SECTION 4 THE LIFE HISTORY AND ECOLOGICAL BEHAVIOUR OF NOTHOFAGUS SOLANDRI

4.1. INTRODUCTION

A number of detailed studies have been carried out on the regeneration of Nothofagus solandri in the Craigieburn Range and at Mt Thomas in North Canterbury, and in the Kaweka Range in the central North Island. Detailed studies have been carried out on the growth of the species in the Craigieburn Range, while supplementary studies on tree growth and on stand growth and structure have been carried out in a number of sites in both the North and South Islands. The methods used and the results of each study are summarised in this section. Supplementary information on the species, outside the specific range of the described studies, is also included where it is felt that its inclusion helps to provide a fuller account of the life history and behaviour of the species.

This section is divided into two main sub-sections. The first describes the regeneration of the species, the second describes tree growth and mortality and stand growth and structure. Each sub-section may be further sub-divided. For instance, 'Regeneration' is described under the headings of 'Flowering', 'Seeding', 'Seed Dispersal', 'Germination and Early Seedling Development', 'Subsequent Seedling Development' and 'Vegetative Reproduction'. Where applicable, under these headings, the range of behaviour of the species is given, and an attempt is made to relate this variation to site. For instance, the ~~influence of~~ altitude is described and examples are

sometimes given as to how the behaviour may vary from one Nothofagus solandri association to another.

4.2. REGENERATION

4.2.1. Flowering

Nothofagus solandri is monoecious, but the staminate and pistillate flowers are borne on the same vegetative shoot as it expands from the opening bud. The flower primordia are formed in the dormant buds during the summer and appear in the following spring. Thus there is a period of twelve months during which internal development proceeds. As the flowering bud opens in the spring, peduncles bearing usually 1-3 staminate flowers appear singly in the axils of the uppermost scales or lowermost leaves which lie near the top of the bud. Immediately above the staminate flowers sessile or subsessile pistillate inflorescences are borne singly in the axils of the leaves. Above these, a normal leafy shoot develops with minute vegetative buds in the axils of the leaves (Poole, 1950 Pt. I). The pistillate flowers are receptive at about the same time as pollen is shed from the staminate flowers on the same shoot (Poole, 1950 Pt. 2). Pollination is effected by wind.

It is normal for Nothofagus solandri to show a marked tendency to periodicity in flowering, and it has been suggested by Poole (1949) that flowering is less frequent at higher altitudes. Towards the coast in Canterbury however, trees have been observed to flower moderately heavily twice in one season. 20-30 year old trees, which had been transplanted as seedlings from the Canterbury foothills to Rangiora, as saplings flowered in September 1964 and again in March 1965.

Flowering has been observed in mountain beech on seedlings as young as six years of age but seed did not set. Flowering to produce viable seed may occur on 25- to 30-year old, open grown trees and it is possible that it occurs even earlier.

The time of both flowering and pollination is influenced by altitude. In the summer of 1966-67 flowering occurred in late October and early November at 1500 feet altitude in the Canterbury foothills. At around 3000 feet in the Craigieburn Range, however, it did not occur until mid-December and at 4500 feet, near the bushline it was further delayed until early January. Thus in this particular season there was a $2\frac{1}{2}$ month delay between flowering at 1500 feet and at 4500 feet, almost a delay of 1 month per 1000 feet.

4.2.2. Seed Shed

Sixty-four funnel shaped metal seed trays, each with a catch area of three square feet, were installed in reasonably pure Nothofagus solandri forest at the beginning of 1965 (for design see Fig. 16). These trays were arranged in eight lines, each of eight trays. Three of these lines were installed in the Kaweka Range in the central North Island and the remaining five were placed in the Craigieburn Range in North Canterbury. In early 1966 a further line of eight trays was installed at Mt Thomas. For a description of the site and of the forest at the location of each seed tray line see Table 3.

The eight seed trays in each line were placed at intervals of 2 chain apart along the contour. This distance was chosen on the assumption that seed would be unlikely to travel as far as one chain distance through the forest and thus it would be unlikely that any

Fig. 16 - A seed tray installed in position at 4400 feet altitude in the Craigieburn Range. Note the funnel shape, designed to direct seed to outlet at the bottom. A removable canister is placed over this outlet and catches the seed, litter, etc. It is removed and replaced at time of collection.

two trays would be fed from the same trees. The total length of each line of seed trays was around 14 chains.

An opening at the bottom of each funnel shaped tray leads to a removable fine gauze-bottomed plastic canister (see Fig. 16). It is into this canister that the contents of the seed tray settles. These canisters were removed and replaced by empty canisters at approximately monthly intervals but sometimes as a result of bad weather, or for other reasons, collection time had to be delayed, and particularly in the case of the Kaweka trays, the interval between collections sometimes extended to more than two months. After

collection, the contents of each individual tray was sorted for Nothofagus solandri seeds which were then counted and cut to test for soundness. Sound seeds were counted and the percent soundness calculated.

Line	Locality	Altitude	Av. aspect	Av. slope	Association	Other Features
A	Craigieburn	4400	NW	35	D1	Dense stand
B	"	3900	NW	30	D1	" "
C	"	3400	NW	25	D1	" "
D	"	3900	SE	30	D1	" "
E	"	2800	NW	35	D1	Fairly open stand
F	Mt Thomas	1800	NW	25	C1 - C3	" " "
AA	Kaweka	4400	NW	35	C6	Dense stand
BB	"	3900	NW	30	C6	" "
CC	"	3400	NW	25	C4	Very open stand

Table 3 - Description of the site and of the forest at the location of each line of seed trays. Altitude is given in feet, aspect and slope are average figures and association refers to the Nothofagus solandri association described in Section 3.

Seed fall was measured during the 1965, 1966, 1967 and 1968 seasons but the collection for 1965 is only partially complete due to the date of installation of the seed trays falling part way through the seed fall period.

Seed collected from the Kaweka lines, AA, BB, and CC, during the height of the 1967 seedfall, from March 30th to May 30th, was sorted into sound seed (that containing ~~endosperm~~) and hollow seed

(with no ~~endosperm~~ embryo). The total sound seed and total hollow seed from each tray was then weighed.

The results of the seedfall and seed soundness studies for each year of collection are given in Table 4. The total seed fall and sound seed fall for each line of trays for each period of collection is given in Appendix 4, while the weight of hollow and sound seed from the Kaweka lines of seed trays is summarised in Table 5.

As has been mentioned in a previous paragraph, Nothofagus solandri shows a marked tendency to periodicity in flowering, and it has been noted also, by Poole (1949), and P. Wardle (1965), that abundant flowering will not necessarily result in abundant seeding owing to the possible intervention of such factors as unfavourable climate at critical periods of development (i.e. late frost at time of flowering and perhaps wet weather affecting pollen dispersal) and possibly insect attack. Consequently there is a marked tendency toward periodicity in seed production. This is well demonstrated with reference to Table 4. For instance, there was over 1000 times as much seed collected in 1967 as in 1966 in line A of the seed trays. In line B there was almost 300 times as much while in line C there was about 22 times as much.

A good seed year is not necessarily country-wide. The 1967 season was good in the Kaweka and Craigieburn Ranges and in fact throughout most regions in the vicinity of the Main Divide, but was a poor seed year in the Canterbury foothills (see Line F, Table 4) and at Tuatapere in Southland. The reverse was the case in 1966 which was a good seed year in Tuatapere and in the Canterbury foothills, but was poor throughout the Main Divide regions.

Year	1965*			1966			1967			1968		
Line	Mean Total	Mean Sound	% Sound	Mean Total	Mean Sound	% Sound	Mean Total	Mean Sound	% Sound	Mean Total	Mean Sound	% Sound
						Craigieburn						
A	6.4	0.0	0.0	0.3	0.0	0.0	348.9	24.4	7.0	1.2	0.0	0.0
B	3.1	0.0	0.0	2.5	0.1	4.0	722.4	211.3	29.2	4.4	0.0	0.0
C	1.3	0.1	7.7	46.0	5.5	12.0	998.3	570.1	57.1	8.5	0.0	0.0
D	1.4	0.0	0.0	6.9	0.3	4.3	753.0	298.3	39.6	3.1	0.0	0.0
E	1.9	0.0	0.0	63.4	5.9	9.3	405.4	184.9	45.6	0.4	0.0	0.0
L.S.D. 5%				39.2	4.2		220.1	149.7		5.8	-	
L.S.D. 1%				52.7	5.6		296.3	201.5		7.9	-	
						Mt Thomas						
F	N.R.	N.R.	N.R.	796.1	268.6	33.7	25.9	5.0	19.3	9.3	1.0	10.8
S.E. (P = 0.05)				391.0	140.8		31.8	6.4		4.7	1.7	
						Kaweka						
AA	15.8	0.0	0.0	8.5	0.0	0.0	2012.8	632.0	33.9	4.9	0.1	2.0
BB	10.6	0.0	0.0	55.0	0.5	0.9	3638.6	2124.1	58.4	5.3	0.1	1.9
CC	4.5	0.0	0.0	156.4	2.0	1.3	2329.3	1309.1	56.2	4.3	0.3	7.0
L.S.D. 5%				147.3	1.6		1291.3	675.7		3.0	0.5	
L.S.D. 1%				204.1	2.2		1794.0	938.7		4.2	0.7	

* The 1965 figures are incomplete. N.R. refers to no record.

Table 4 - Mean total number of seed collected and mean sound seed fall per tray and percent of seed fall which was sound, for each of the nine lines of seed trays, for the years 1965 to 1968 inclusive

Line	Mean Weight per 1000 seed (in lbs)	
	Sound	Hollow
AA	0.0107	0.0034
BB	0.0126	0.0035
CC	0.0122	0.0042
L.S.D. 5%	0.0016	0.0006

Table 5 - Mean weight per 1000 seed of hollow seed and sound seed. There are eight replications. Each seed tray in a line represents one replication.

Previous to this study the determination of a good seed year as distinct from a partial seed year in Nothofagus solandri has been purely subjective (that is with the exception of some work carried out by Poole in the black beech - hard beech forests at low altitudes in the Wairarapa). Past records of seed years are disconnected and in no one locality have continuous records been kept for any length of time. In many cases flowering intensity alone has been recorded, and, as mentioned previously, an abundant flower year does not necessarily result in a good seed year. Frequently seed years have been mentioned in literature but in many cases the species and localities concerned have not been recorded. However, a list of the more reliably recorded seed years from 1936 to the present day is given in Appendix 5 and from this information two tentative conclusions are drawn. These are:-

(a) The average interval between good seed years approximates ten years. For instance, in Canterbury near the Main Divide, four good seed years have occurred since 1936. These were in 1936, 1949, 1957

and 1967, and in northern Westland they have occurred in 1936, 1945, 1952 and 1957. In the Tuatapere area, good seed years have occurred in 1939, 1949, 1954 and 1966.

(b) Between major seed years there are usually a number of partial seed years. These may occur at approximately three year intervals. Thus in Canterbury, between the major seed years of 1957 and 1967, two minor seed years occurred in 1960 and 1963.

Just as the quantity of seed shed may vary considerably from year to year, so may the percentage of seed which is sound. The quality of the seed tends to be much higher in a good seed year than in a poor one (see Table 4). For instance, in 1966 at Line C in the Craigieburn Range, there was a mean fall per seed tray of 46 seed and only 12 per cent of these were sound. In 1967 the seed fall rose to 998 seed per tray and correspondingly the proportion of seed which was sound rose to 57 percent. In the 1968 seed fall the mean number of seed per tray was only 8 and none of this was sound. In every line of seed trays the same pattern held, i.e. heavy seed fall in each case corresponded with high percentages of sound seed and low seed fall corresponded with low percentages of sound seed. The effective difference in terms of regeneration, between good seed years and poor seed years is thus even more marked than total seed fall figures alone would suggest. A good seed year may produce up to 20,000 times as many sound seed as a poor seed year (i.e. Line BB for the years 1967 and 1968).

The highest seed production which was recorded during the present study was in 1967 from Line BB at 3900 feet altitude in the Kaweka Range. Here the mean fall per tray was 3638 seed. As the

area of each tray was 3 square feet this meant that the fall per acre was in the vicinity of 53 million seed. Of this 58 per cent or 31 million seed were sound. The total weight of seed production has been calculated, with reference to Table 5, as 467.6 lbs per acre. On the other hand, the lowest recorded seed fall was from Line A at 4400 feet in the Craigieburn Range in 1966. Here the mean fall per tray was only 0.3 seed. On a per acre basis this would be in the vicinity of 3600 seed only. The seed was not sound and consequently the equivalent weight production per acre would be approximately one hundredth of a pound.

The peak of seed fall occurs some time between March and May, and in fact the proportion of the annual seed fall which occurs outside of the six month period from January to June is negligible. Some seed, however, may fall into the seed trays at any month of the year. This is especially so after a heavy seed fall season (see Appendix 4). The seed which falls in the later half of the year has undoubtedly had its fall interrupted by being caught up in the crook of branches, in spider-webs, etc. Between 70 and 100 percent of the annual seed fall occurred within a two month period in each of the nine seed tray lines and in fact 70 to 80 percent of the total may occur within one month (see Fig. 17).

The time of the peak of seedfall may vary slightly, even within one particular area, from one year to another. It is apparent from Appendix 4 that in the poor seed year of 1966, peak seed fall occurred earlier in both the Kaweka Range and Craigieburn Range than it did in the good seed year of 1967, i.e. in the Kaweka Range in 1966 the peak

production was in March. In 1967 it was in April - May. In the Craigieburn Range, in 1966 it was in March - April while in 1967 it was in April. In the poor seed year of 1968 it again occurred early in both areas. It may well be that seed fall occurs earlier in poor seed years than in good seed years.

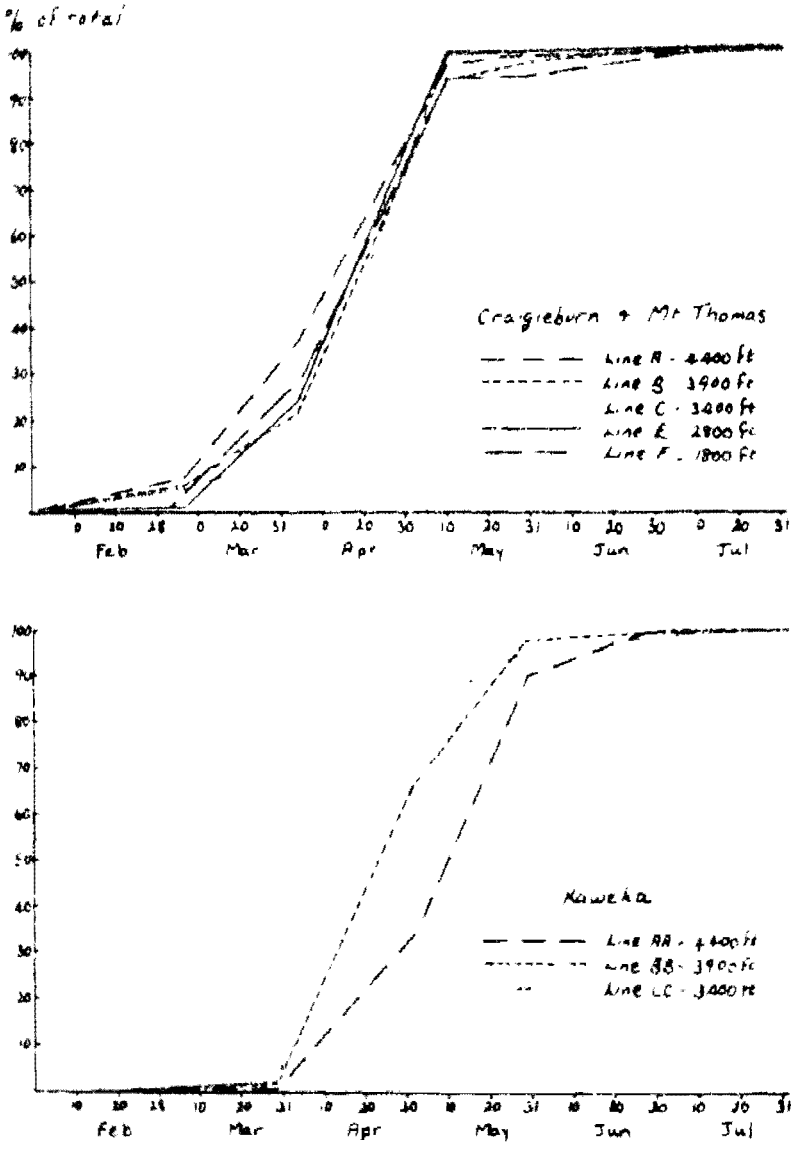

Fig. 17 - Accumulative percent seed fall for eight of the nine lines of seed trays for the 1967 season.

The pattern of sound seed shed follows that of total seed shed, in that the highest proportion of sound seed falls during the peak

months of seed fall (see Fig. 18). Seed shed previous to, or following the peak fall, has a considerably lower proportion of sound seed than seed shed during the peak. The fall-off in the proportion of sound seed prior to the peak tends to be more rapid than the fall off following the peak.

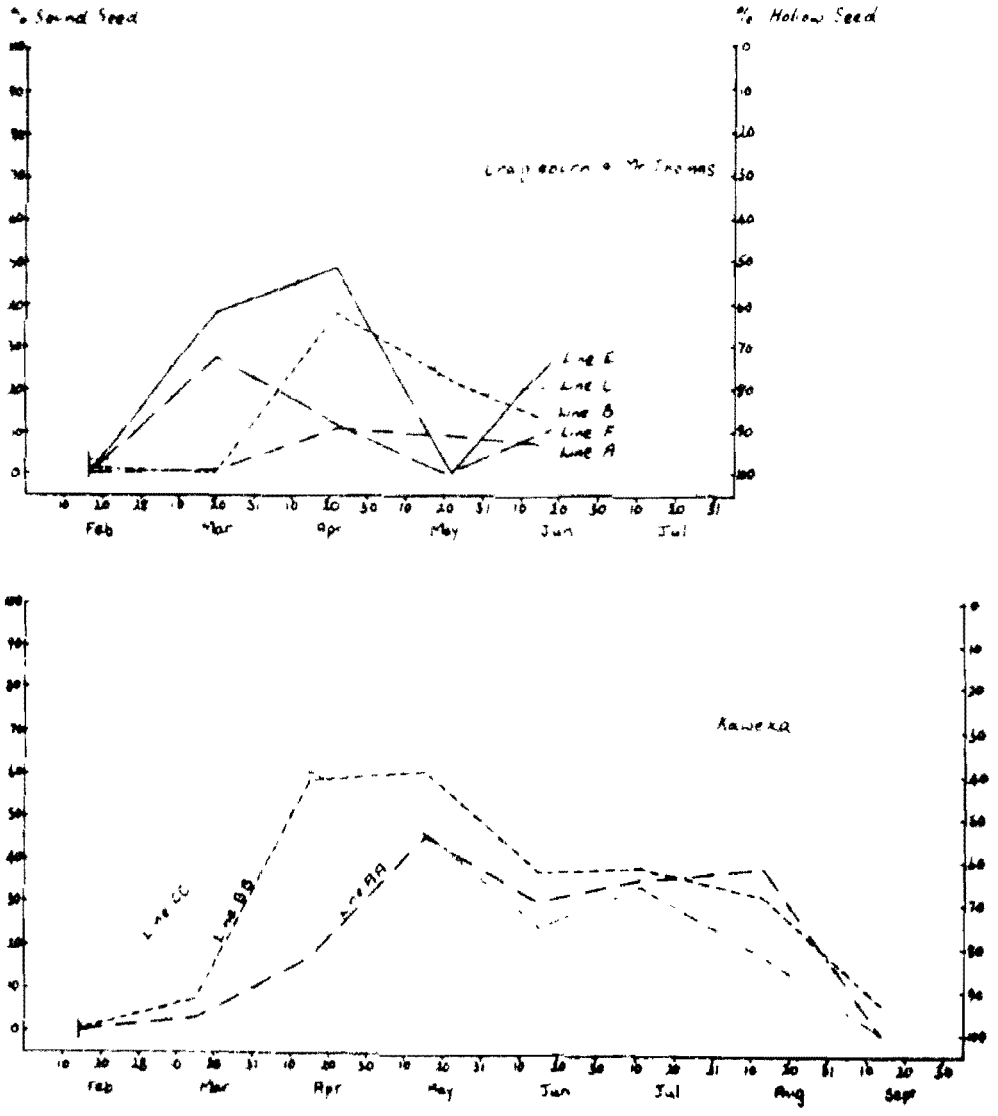

Fig. 18 - Proportion of seed fall which was sound and hollow for each collection period of the 1967 season for eight of the nine lines of seed trays.

Similar studies on other tree species have shown a relationship between quantity of seed fall and quality of the site. For instance,

Sarvas (1962), with Pinus sylvestris, showed that there was an increase in the annual seed crop with increase in site fertility as measured by tree dominant height. Table 4 demonstrates that Nothofagus solandri behaves in a similar fashion. Seed tray lines A, B and C in the Craigieburn Range differ in altitude but are on the same slope, are in stands of similar structure and age, and belong to the same association, D 1. For each complete year of collection, the lower altitude line, C, received more than twice as much seed as line A, which is at 1000 feet higher altitude and is located close to the bushline. Line B, the mid-altitude line, received an intermediate seed fall each year. Line E, though, which is the lowest altitude line in the Craigieburn Range, received a lower overall seed fall than either line B or line C, but it is located some distance from the other three lines and is on a dry, steep, rocky face. The stand is fairly open and the predominant height of the stand, which may be regarded as an indicator of site quality, is less than in either lines B or C. Lines B and D are at the same altitude in the Craigieburn Range and the stands feeding them are similar but are on opposing aspects. Line D is on the cool, south-east aspect and line B is on the warm, north-west aspect, yet the seed fall in each is similar. In the Kaweka Range, line AA, which is located close to bushline, again received less seed than the mid-altitude line, BB, but there was a reduction in the quantity of seed collected in line CC which is at a yet lower altitude. This was almost certainly due to the very open nature of the lower stand. The Mt Thomas line, F, is located in the ecotone between the two Nothofagus solandri associations, C 1 and C 3. Association C 3 represents a better site quality than

Association C 1 (see Section 2), and the seed fall in the individual seed trays improved towards Association C 3 (see Fig. 19).

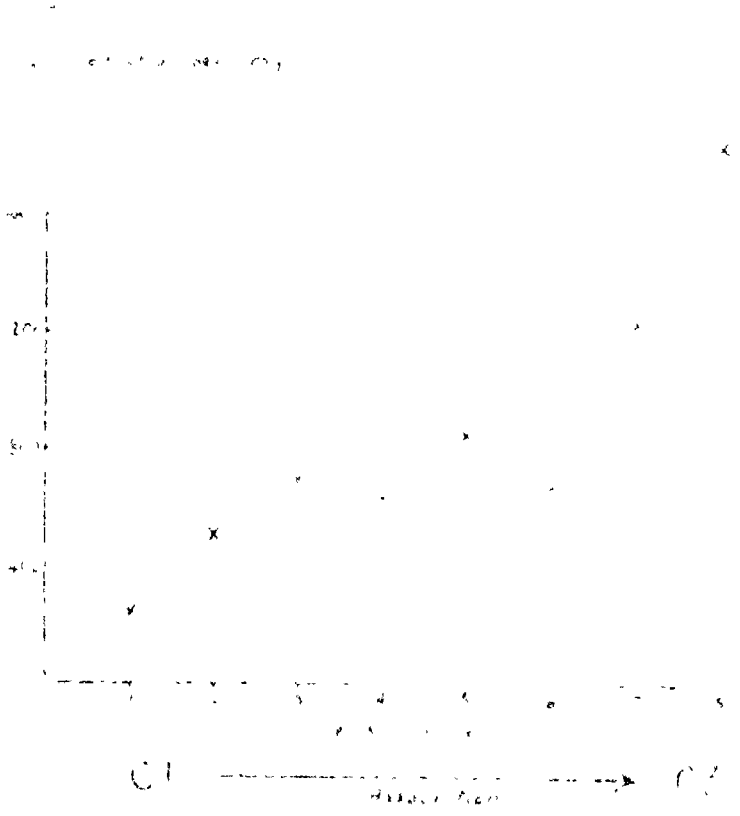

Fig. 19 - Total seed production per tray for the years 1966, 1967 and 1968 at Line F at 1800 feet, Mt Thomas.

Seed quality also shows deterioration with increase in altitude, at least in the higher Nothofagus solandri forests. For instance the per cent sound seed from line A in the Craigieburn Range in 1967 was only 7.0 but at line B it was 29.2 and at line C it was 57.1. In the Kaweka Range, in the same year, the seed was 33.9 per cent sound at line AA, 58 per cent sound at line BB and 56.2 per cent sound at line CC. However, whereas a less favourable site, even at the same altitude, shows a marked deterioration in the quantity of seed produced, seed quality does not seem to be affected to the same degree. For instance, at line F, at 1800 feet at Mt Thomas there was little

change in seed quality from tray to tray even though the total seed fall per tray increased considerably from the poor Association C 1 sites towards the better C 3 sites (see Fig. 19). Line B is located in a stand at 3900 feet altitude and line E, in a stand at 2800 feet altitude in the Craigieburn Range. The predominant height of the line B stand is greater than for the line E stand and presumably the former represents a better site for growth of Nothofagus solandri even though it occurs at a higher altitude. The mean seed production per seed tray in 1967 in line B was 722.4 compared with 405.4 in line E but the percent of the seed which was sound in line B was only 29.2 as compared with 45.6 in line E (see Table 4). Also of importance in relationship to the effect of site on seed quality is the apparent decrease in the mean weight of both the sound and the hollow seed with increase in altitude. This is demonstrated for the 1967 seed fall in the Kaweka Range by Table 5.

It has been mentioned in the previous subsection that the time of flowering may be delayed almost 1 month per 1000 foot increase in altitude and Fig. 17 demonstrates that a similar delay in the time of seed fall can occur, i.e. in the Kaweka Range, in the good seed year of 1967, the peak occurred between the 30th March and the 1st May at 3400 feet but not until the 1st of May to the 30th May at 4400 feet. However, there may be no discernible delay at all, i.e. in the Craigieburn Range in the same season, which was a good seed fall season also, all the lines from 2800 feet to 4400 feet had their peak seed fall between the 4th April and the 10th May and even in the Mt Thomas line at 1800 feet altitude, the peak was between the 5th April and the 10th May. In this particular case the period for the

development and ripening of seed must have been considerably shortened at the higher levels of altitude.

The study has not been under way for a long enough period to evaluate the influence of altitude and other site factors in the determination of the interval between good seed years or on the relative seed fall between good and poor seed years. There is a suggestion, however, that the difference between good and poor seed years may become more marked with increase in altitude. For instance, in the Kaweka Range there was 237 times as much seed produced in the good seed year of 1967 than in the 1966 season. At 3900 feet this figure had reduced to 66 times while at 3400 feet there was only 15 times. There was a similar pattern in the Craigieburn Range for the same two seasons. At 4400 feet there was 1396 times as much seed produced in 1967 as in 1966. At 3900 feet altitude there was 275 times as much in line B and 112 times as much in line D. At 3300 feet this figure had reduced to 22 times and at 2800 feet there was only 6 times the amount of seed produced in 1967 as in 1966. This pattern did not hold though for the 1967/1968 comparison.

4.2.3. Seed Dispersal

In discussing dispersal distances for a species it is necessary first to distinguish between chance dispersal which refers to freak occurrences, and normal dispersal. It is also necessary to distinguish between the effective distance of seed dispersal, which is the distance from the seed source to which regeneration may be found and the actual dispersal distance which is the distance to which seed capable of germination normally travels. For instance, the actual

dispersal distance from seed trees growing in grassland and in tall scrub may well be the same, but whereas in the grassland it is rare to find regeneration further than tree height away from the nearest seed tree in the tall scrubland regeneration may be found further than ten times tree height away from the nearest seed tree (see Fig. 20). Thus even though the actual dispersal distance is the same in each case, the effective distance is very different.

Fig. 20 - Effective dispersal distances. A. Ashley Gorge, North Canterbury. Where the seed trees are surrounded by grassland it is rare to find regeneration further than tree height away from the parent tree. B. Mt Thomas, North Canterbury. Where the seed trees are surrounded by tall scrub, regeneration may be found further than ten times tree height away from the nearest seed trees.

The various agencies of seed dispersal in Nothofagus solandri worthy of consideration are as follows:-

(a) Wind. The nut of Nothofagus solandri is small, seldom exceeding 7 mm in length, and the sound seed is comparatively heavy for its size and though it is supplied with small wings it can not

be considered to be well adapted to wind dispersal. However, wind must be an important factor as wind gusts over 100 m.p.h. are not unusual at the higher altitudes in Nothofagus solandri forest. There is little doubt that wind is the main agency for normal dispersal at least to distances as far as 10 chains.

(b) Birds. Birds, especially of the finch types, feed on sound seed of Nothofagus solandri but the ~~endosperm and~~ embryo of the seed is digested and consequently they cannot be considered as important agencies for dispersal. They may possibly aid in chance dispersal by transport of seed in their feathers.

(c) Water. Riparian stands of Nothofagus solandri are quite common throughout other forest types where there is a seed source of the species further upstream. This suggests some form of water dispersal. However, this phenomenon may well result from a facility of the species to pioneer bare ground and eroded banks resulting from stream activity, the newly-formed surfaces constantly providing a niche for Nothofagus solandri to become established and perpetuate itself within a vegetation zone that would otherwise be closed to it.

4.2.4. Germination and first year seedling development

Study of the germination and first year seedling development involved the layout and measurement of the three trials, 'a', 'b' and 'c', described below.

Trial 'a'. Natural germination and first year seedling development under stand conditions were studied on 2 feet x 3 feet plots in the vicinity of the seed tray lines A, B, and C, at 4400, 3900 and 3400 feet altitude in the Craigieburn Range. For description of the

stands, see Table 3. Eight plots, each in the vicinity of a seed tray, were selected for each of these sites and in each plot all the existing advance growth seedlings were removed. Following the 1967 seedfall, which was reasonably good in the Craigieburn Range, the plots were observed for germination at approximately weekly intervals. At each visit, a count of the number of first year living and first year dead seedlings was made. The dead seedlings were then removed to prevent their being counted twice. At the end of the first summer of growth, the stage of development reached by the seedlings at each site was noted.

Trial 'b'. Seed gathered from Nothofagus solandri, from 1500 feet altitude in the Rakaia catchment was sown in 1966 under a range of shade and soil treatments at 3200 feet and 4400 feet in the Craigieburn Range and at 150 feet altitude at Rangiora. At 3200 feet, four shade treatments were used, the first (shade 1) utilising full light, and the remaining three (shades 2, 3 and 4) employing one, two and four thicknesses of sarlon mesh. One thickness of sarlon mesh is approximately equivalent to 36 percent of full light (see Fig. 21). At 4400 feet in the Craigieburn Range, and at Rangiora, only two shade treatments were used. These were full light and one thickness of sarlon mesh.

Five soil treatments were used at 3200 ft in the Craigieburn Range. These were, mountain beech forest top soil with litter mixed, forest top soil with raw litter removed by sieving, two grades of subsoil, one with a finer texture and hence heavier than the other, and scree material in which the larger rock particles had been removed. At 4400 feet in the Craigieburn Range, and at Rangiora, only three soil

treatments were used. These were forest top soil with litter mixed, the lighter subsoil, and scree.

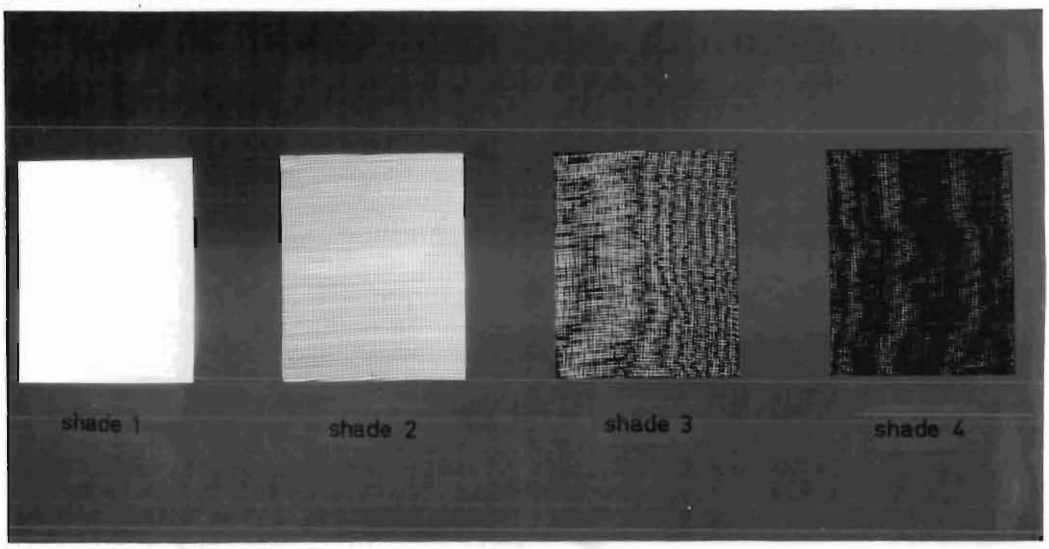

Fig. 21 - The four shade treatments employed in Trial 'b'. Shade 1 is full light and shade 2, 3 and 4 employ respectively 1, 2 and 4 thicknesses of sarlon mesh. (Photo by K. Platt).

The full range of soil treatments at each site were employed in the open, but with one exception, only the forest top soil with litter treatment was employed under the shades. This exception was at 3400 feet, where, under one thickness of sarlon mesh, light subsoil was also used.

For each separate treatment there were four randomly placed replications and for each replication a batch of 200 seed was sown. Samples of this seed were tested by cutting and gave a mean soundness percent of 47.

This experiment was laid out in August 1966 and following the first germination, counts of the number of living and number of dead seedlings were made for each replication of each treatment at approx-

imately 3 to 4 day intervals up until May 1967. Dead seedlings were removed after each count to ensure that they were not counted twice.

This experiment was set up without the knowledge that there was going to be adequate natural seeding in the Craigieburn Range in 1967 for trial 'a' to be carried out. Consequently there is a certain degree of repetition, but this trial still serves the purpose of giving some idea of germination behaviour under a range of controlled shades and soil types and therefore the results are included.

Trial 'c'. In order to follow the pattern of germination and early seedling development more closely, seed gathered from 1500 feet altitude in the Rakaia catchment was sown in 1966 on nursery mulch and germinated under glasshouse conditions at Rangiora. The pattern and rate of seedling development was kept under observation and initially at two weekly intervals, but later at monthly intervals, several of the most advanced seedlings were uplifted and examined. The number of days taken for the radical to appear and for the cotyledons and first foliage leaves to emerge, and other developments to take place was recorded.

The results of each seedling count in trials 'a' and 'b' are summarised in appendices 6 and 7, while total germination and mortality for the first season are given below in Tables 6 and 7. The results of trial 'c' are simply discussed in the relevant paragraphs of the text.

The seed from Nothofagus solandri may germinate soon after it is shed. For instance, heavy prewinter germination was observed in May up to altitudes of about 1800 feet in the Northern Ruahine and Aorangi Ranges following the partial seedfall of March 1963. However,

Line	Altitude (in ft)	Sound Seed Mean	Germination Mean	%	Prewinter Mort. (24 Apr) Mean	%	1st year Mort. (27 Nov) Mean	%
A	4400	24.4	1.3	5.1	1.1	84.6	1.1	84.6
B	3900	211.3	20.6	9.7	16.1	78.2	17.8	86.4
C	3400	570.1	115.3	20.2	66.1	57.3	73.5	63.7

Table 6 - Results of trial 'a'. Mean sound seed fall per tray and mean germination and mortality of first year germinates per plot. The percent germination figures assume that each line of plots received the same quantity of sound seed as did the eight related seed trays.

only post winter germination has been observed in the Kaweka Range, in the Craigieburn Range and at Mt Thomas. It would seem that prewinter germination is restricted to low altitudes in the North Island and maybe in the northern South Island but that elsewhere post winter germination is the rule. The onset of germination usually occurs sometime from September to December dependent on altitude (see Fig. 22, App. 6 and App. 7). The onset of germination in trial 'b' at 150 feet altitude at Rangiora in 1966 was between September the 20th and 22nd. At 3200 feet in the Craigieburn Range it was between the 25th and 28th of October and at 4400 feet it was between the 1st and 6th of December. Following the 1967 seed year in the Craigieburn Range, the first germination at 3400 feet altitude occurred between the 17th and 25th of October, at 3900 feet between the 25th of October and 1st of November and at 4400 feet, between the 22nd and 30th of November. There is apparently a [redacted] month delay in the time of germination for the 4250 feet increase in altitude. Increase in shade also resulted

TREATMENT	SITE		
	Rangiora 150 ft	Craigieburn 3200 ft	Craigieburn 4400 ft
Forest Top Soil + Litter	Mean Germination (Number)		
Shade 1	4.3	0.0	0.0
Shade 2	54.0	4.0	1.5
Shade 3	n.t.	3.5	n.t.
Shade 4	n.t.	2.3	n.t.
L.S.D. 5%	27.8	2.7	3.8
Shade 1	Mean Germination (Number)		
Forest Top Soil + Litter	4.25	0.0	0.0
Light Subsoil	10.0	0.3	0.8
Scree	1.0	0.0	0.0
Heavy Subsoil	n.t.	0.0	n.t.
Forest Topsoil - Litter	n.t.	0.3	n.t.
L.S.D. 5%	6.7	0.8	1.6

TREATMENT	SHADE		
	1	2	Difference
	Mean Germination (Number)		
3200 feet. Light Subsoil	0.3	5.0	*** (t-test)

TREATMENT	SOIL		
	Forest topsoil + Litter	Light subsoil	Difference
	Mean Germination (Number)		
3200 feet. Shade 2	4.0	5.0	n.s. (t-test)

Table 7 - Results of trial 'b' Mean germination per treatment. Each treatment consists of 4 replications and for each replication 200 seed (47 percent sound) were sown. (n.t. = no trial).

in a delay in the time of onset of germination at the 3200 and 4400 feet sites, in trial 'c' (see App. 7). It seems that these delays may be related fairly closely to soil temperatures. From thermometers kept, near the artificially seeded germination trials at Rangiora in 1966 and near the natural germination plots at 4400 feet and 3400 feet in the Craigieburn Range in 1967, it was seen that the onset occurs when the 4 inch daily maximum soil temperatures as measured between 9 a.m. and 10 a.m. consistently rise above 44 or 45°C.

Once the first seedlings have appeared, germination usually proceeds fairly rapidly, though it tends to occur more rapidly at the lower altitudes.

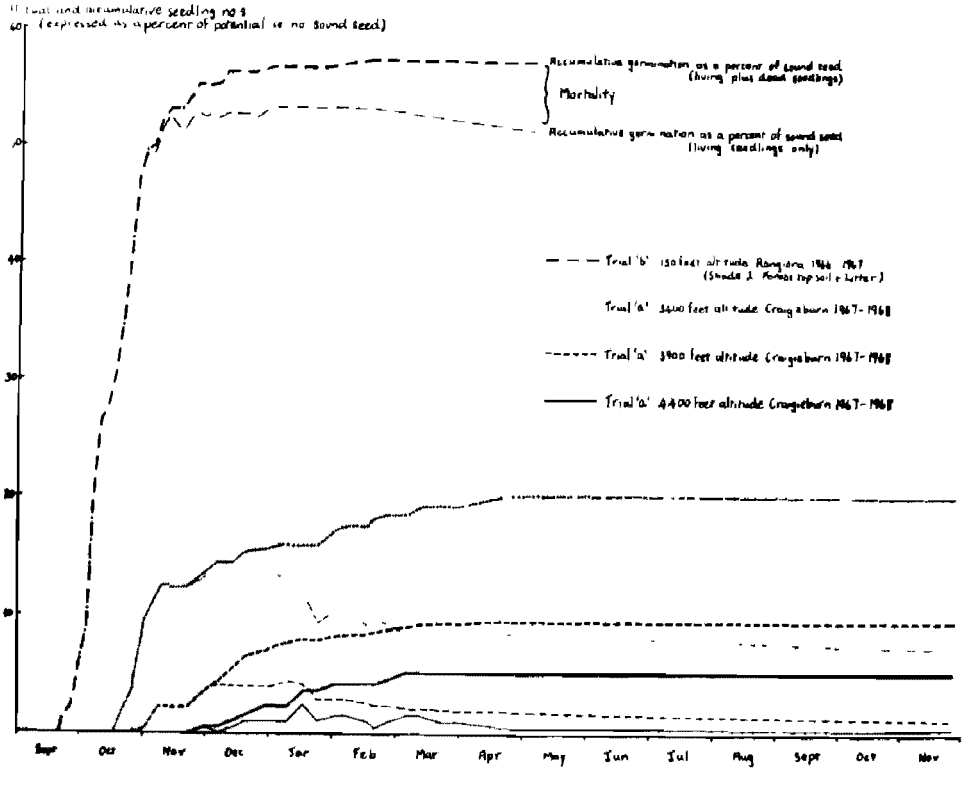

Fig. 22 - Accumulative sound seed germination percentages, and actual seedling numbers as a percent of potential seedling numbers throughout the first season following seeding.

This is apparent from the slope of the graphs in Fig. 22. At Rangiora in 1966, three-quarters of the germination had occurred within 32 days. However, the same proportion of germination at 3400, 3900 and 4400 feet altitude in the Craigieburn Range, after the 1967 seed fall, took 62, 70 and 73 days respectively. Germination continues spasmodically until April. There is no evidence for seed germinating in the following spring.

The highest percentage of germination recorded in the present study was at Rangiora in 1966 under light shade conditions (see Trial 'b'). In this trial 57.4 percent of the sound seed germinated. The germination percentages vary considerably from site to site. Both trials 'a' and 'b' showed a decrease in germination percentages with increase in altitude. In trial 'a' the percent germination of sound seed under canopy at 4400, 3900 and 3400 feet was 5.1, 9.7 and 20.2 percent respectively (see Table 6). The mean number of seed germinating in trial 'b', on forest top soil, under shade 2 conditions at 150, 3200 and 4400 feet altitude was 54.0, 4.0 and 1.5 (see Table 7). There was better germination in nearly every treatment at lower altitudes. There was also quite a marked contrast between the number of seed germinating in the open, and under light shade, at each altitude (see Table 7). In trial 'b' at 3200 feet and 4400 feet, very few seedlings germinated in the open. At 150 feet at Rangiora there was a higher rate, but the only open treatment which gave some germination at all altitudes was the light subsoil treatment. Shade and probably also the subsoil treatments might be expected to retain moist conditions for longer periods than open conditions and the other soil treatments and the tendency for better germination under these condi-

tions suggests that the seed requires a prolonged period of moist conditions before germination can take place and can probably not tolerate drying out of the germination media during the initial stages of germination.

The time taken for germination and the rate of development of young seedlings under moist, warm conditions was studied in trial 'c'. The development (see Fig. 23) was as follows. Seed sown on the 9th August 1966 started to produce a radicle ten days later, on the 19th August. By the 5th September the cotyledons had emerged from the seed coat but from the 5th September until the 19th September no new developments took place other than elongation of the radicle and plumule and full extension of the cotyledons. By the 30th of September, however, the first pair of foliage leaves had appeared, and by

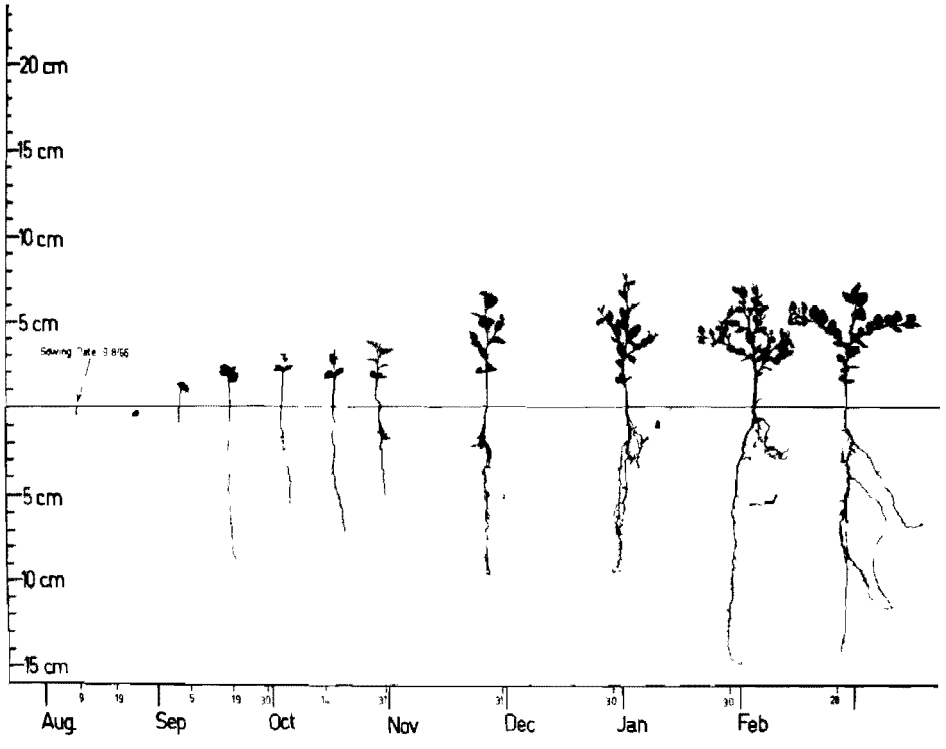

Fig. 23 - Rate of development under glasshouse conditions at Rangiora. (Photo by K. Platt).

the 31st October the seedlings had reached a 6-leaf stage of development and had started to develop lateral rootlets. From this stage on development speeded up. By the 31st November, lateral branches had appeared and the seedlings had a well developed rooting system and by the 30th of January second order branches had been produced.

Changes in altitude and in the degree of overshading can have considerable influence on the stage of development reached by seedlings in the first growing season. At low altitudes, in full light but under conditions of good soil moisture, development similar to that shown in Fig. 23 can be achieved, but at 4400 feet altitude, under the parent Nothofagus solandri canopy, the largest seedlings only reach a 2 foliage leaf stage and stem extension is usually less than 3 cm. In the open, though, they may reach a 5 foliage leaf stage. The differences in the stage of development reached in the open and in the shade, and between different altitudes is demonstrated in Fig. 24.

Prewinter seedling mortality rates are usually fairly high but tend to be higher at high altitudes than at low altitudes and under open conditions than under shade. The prewinter seedling mortality for trial 'a' at 4400 feet was 84.6 percent of all germinated seedlings, at 3900 feet was 78.2 percent and at 3400 feet was 57.3 percent (see Table 6). The best survival recorded in the present studies was under shade at Rangiora where 78 percent of the seedlings which germinated survived the first summer. During the same period, at Rangiora and on the same soil, but in the open, all of the 17 seedlings which germinated died (see App. 7). In fact only 8 seedlings out of the 61 which germinated in the open, in all the soil treatments

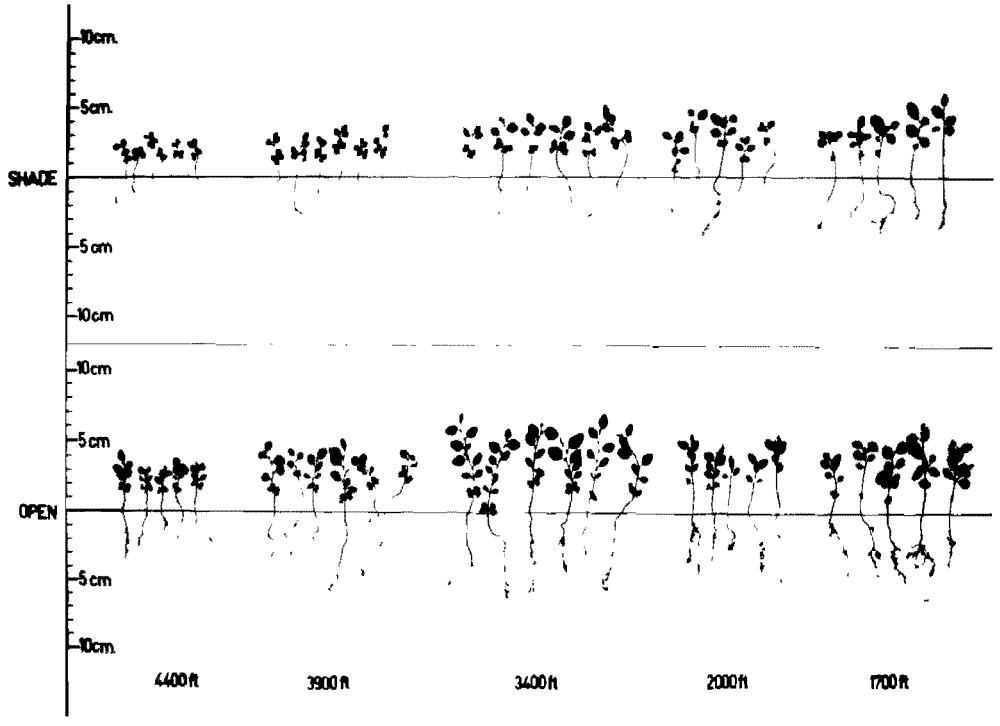

Fig. 24 - Stage of development reached by seedlings of Nothofagus solandri during the first growing season, in the open and under the canopy at range of altitude. (Photo by K. Platt).

at this site, survived the first growing season. The greatest rate of mortality is during the three month period from January to March (see Fig. 22) while during the winter months, it is considerably less. This difference may be due to the seedlings being more susceptible to the summer fluctuations in soil moisture than to the low temperatures existing in the winter months, but partly it would be due to the weaker seedlings having succumbed before the winter has started. One quite important cause of 1st year seedling mortality observed near bushline in the Craigieburn Range is related to litter movement on steep slopes following rain. Many seedlings become buried by litter while others have soil and litter removed from around

their roots.

4.2.5. Subsequent seedling growth and mortality

Two experiments were set up to study the growth of seedlings of Nothofagus solandri more than one year old. The first trial 'a' was designed to study absolute height growth and mortality rates of naturally growing seedlings at a range of altitudes, under an intact canopy of adult trees and where the canopy had recently been removed. The second, trial 'b', was designed to study in detail relative growth patterns of advance growth seedlings transplanted to a range of soil, shade and altitude treatments. The two trials are described below:-

Trial 'a'. Eight plots, each 2 feet x 3 feet in area were demarcated in the vicinity of the seed tray lines A, B and C at 4400 feet, 3900 feet and 3400 feet in the Craigieburn Range. For description of the stands at these sites see Table 3. In the vicinity of each of these three seed tray lines, all trees in an area 2 chain x 2 chain had been ringbarked during the 1965-66 summer. In each of these three areas a further eight 3 feet x 2 feet plots were demarcated. In these plots all the existing advance growth seedlings on the forest floor were marked and the height of a randomly chosen proportion of these seedlings was measured. The plots were first measured following release, in the summer of 1965-66, and were remeasured two years later in the summer of 1967-68, and the percentage mortality and rate of growth was calculated.

The original height of the majority of the seedlings was between 1 inch and 5 inches and their age, as established from ring counts of seedlings on adjacent sites was usually seven to eight years though a

small percentage were as old as twenty-five years or as young as three years.

Trial 'b'. This trial was carried out concurrently with trial 'b' of germination and early seedling development. Advance growth seedlings, seven to eight years old, were taken from under a moderately dense stand of Nothofagus solandri at 4000 feet altitude in the Craigieburn Range, in the early winter of 1966. Their roots were gently washed of soil, they were shaken dry and then weighed and placed into one of six groups dependent on their green weight. The green weight classes were from 0.2 to 0.25 gms, 0.25 to 0.3 gms, 0.3 to 0.35 gms, 0.35 to 0.4 gms, 0.4 to 0.45 gms and 0.45 to 0.5 gms. Any seedlings under 0.2 gms or over 0.5 gms were discarded. The seedlings were then arranged into batches of 27 and each batch contained six seedlings from the first weight class, five from each of the 2nd and 3rd classes, four from each of the 4th and 5th weight classes and three from the 6th weight class. Each batch of 27 seedlings represented one replication for a treatment and for each treatment four replications were used. With one exception the treatments were those described for the germination and early seedling development trial. The only change was that under shade 2, at 3200 feet altitude a scree treatment replaced the subsoil treatment. Twelve of the groups of 27 seedlings were kept aside but the remainder were planted into the appropriate soil in 6 inch x 3 inch plastic bags with one seedling in each. Each batch of 27 was placed in a box which was then, in turn, placed under the appropriate shade treatment at the appropriate altitude (see Fig. 25).

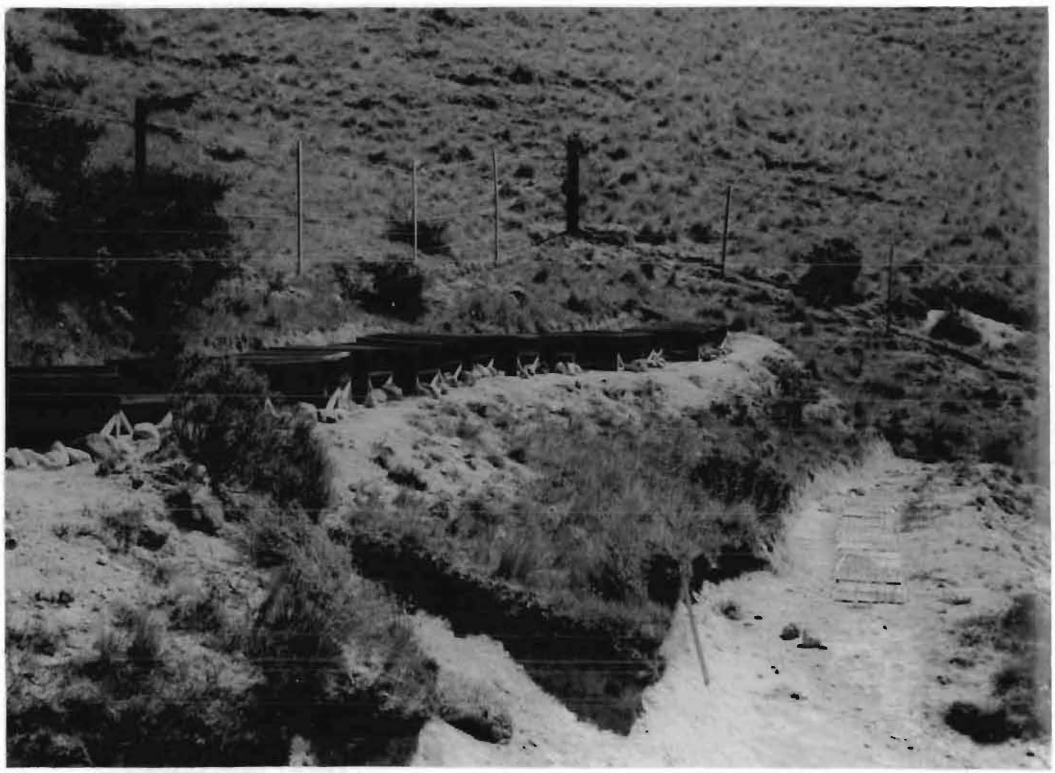

Fig. 25 - Layout of trial 'b' at 3200 feet in the Craigieburn Range.

The twelve groups of 27 seedlings which were kept aside were used as a control and were measured for root length and shoot length. The leaves of each seedling were then removed and counted and leaf areas were measured by a machine at Lincoln College which employs a modification of the dot grid system using air suction. The roots, shoots and leaves were oven dried at 95°C and weighed separately. The means of each of these measurements was calculated for each of the green weight classes and these means assumed as the starting points for the equivalent green weight class seedlings which had been planted out.

At the end of the first growing season after transplant, counts were made of the number of seedlings surviving in each replication of

each treatment and half of the surviving seedlings were harvested. Survival percentages for each replication and total dry weight increases for each seedling were calculated, and the three seedlings from each replication of each treatment which gave the highest total dry matter production were used for analysis of total root and total shoot length growth, increase in leaf area and leaf number and increase in dry weight of root, shoot and leaf. Leaf area in this case was measured by employing dot grid counts on life size photographs of the leaves as the air suction method proved difficult to operate on rigid leaves such as those of Nothofagus solandri.

The remaining seedlings were harvested at the end of the second growing season and the growth of the best three seedlings from each replication of each treatment again calculated.

The calculation of the growth was restricted to the best seedlings in each replication in order that the comparisons between seedlings from different treatments would be more meaningful, i.e. if in one treatment all seedlings had survived while in another treatment a small percentage only had survived, it is likely that the small percentage would be the basically healthier seedlings and that it would have been mainly the weak seedlings which had died. The mean growth for the treatment with the better survival would be relatively lowered by the inclusion of the weaker seedlings.

The results of Trial 'a' are given below in Table 8. First year percent seedling survivals for Trial 'b' are summarised in Table 9. Second year survival percentages are not given as they are largely meaningless, having been complicated by harvesting and mortality in the first year. The first year figures can be used for com-

parative purposes only as they are influenced by early mortality resulting from transplant. They are useful in that they provide a comparative estimate of the ability of the seedling to survive certain conditions of soil, altitude and shade. Growth increases in Trial 'b' are summarised in Table 10. More detailed information including original weight and numbers etc. and percentage increases is given in Appendix 8.

Seedlings of Nothofagus solandri can persist for quite long periods under a dense parent canopy without making a great deal of height growth. Some such seedlings have been aged by ring counting and found to be over twenty years old when still no more than 6 inches or 8 inches high. Table 8 demonstrates the slow growth rate of these 'advance growth' seedlings under a dense canopy. For instance, near bushline at 4400 feet in the Craigieburn Range, the mean increase in length of the leading shoot over a two year period was little over 0.1 inches. The average annual growth in this case would be 0.06inches, and even at 1000 feet below bushline the average annual growth was only 0.6 inches. Where the canopy had been opened up, the mean growth was three to seven times better but even so it did not exceed 1.7 inches per year. However, the growth of the best of the seedlings at the 3900 feet and 3400 feet altitude sites in the trial was up to 6 inches per year, and seedlings of similar size have been observed growing at rates of up to 18 inches per year.

The rate of seedling mortality is far less for these older seedlings than for the first year seedlings. For instance, 341 of the 2119 advance growth seedlings originally counted died during the two year period over which the trial was run. This represents a 16

	Height Growth (inches)								Mortality			
	Open canopy				Dense canopy				Open canopy		Dense canopy	
Altitude (in ft)	Sample Size	Mean	S.E.	Max.	Sample Size	Mean	S.E.	Max.	Sample Size	%	Sample Size	%
4400	22	0.88	0.21	1.5	56	0.12	0.04	1.5	39	44	166	25
3900	131	3.42	0.52	12.0	23	0.55	0.27	2.0	205	19	41	39
3400	142	3.23	0.32	9.5	258	1.20	0.13	5.5	714	20	954	9

Table 8 - Mean height growth and maximum height growth of seedlings under open and dense canopied stands for the two year period from autumn 1966 to autumn 1968. The size of the sample in each case is given (S.E. is for P = 0.05).

SHADE	SOIL	ALTITUDE (FT)					
		150		3200		4400	
		Mean % Survival	S.E.	Mean % Survival	S.E.	Mean % Survival	S.E.
1	A	28.1	3.8	48.0	3.1	50.0	4.9
2	A	89.2	5.7	76.0	4.0	63.6	14.2
3	A	n.t.		69.5	15.4	n.t.	
4	A	n.t.		58.4	15.8	n.t.	
1	A	28.1	3.8	48.0	3.1	50.0	4.9
1	B	n.t.		58.4	14.7	n.t.	
1	C	66.7	5.1	61.2	9.3	62.1	14.0
1	D	n.t.		53.7	13.4	n.t.	
1	E	2.8	12.7	16.7	15.4	24.1	22.8
1	E	2.8	12.7	16.7	15.4	24.1	22.8
2	E	n.t.		58.9	4.0	n.t.	

Soil A - Forest top soil with litter
" B - Forest top soil with coarse litter removed
" C - Lighter subsoil
" D - Heavier subsoil
" E - Scree

Table 9 - The mean percent survival at the end of the first year following transplant. Trial 'b' (S.E. is for P = 0.05). (n.t. = no treatment).

per cent mortality, or approximately an 8 per cent annual mortality rate. This trial in natural regeneration was not sufficiently large to show up differences in mortality between different altitudes or between open canopy or closed canopy conditions, but some idea of relative mortality under a range of soil, shade and altitude treatment was gained from trial 'b'. The results are summarised in Table 9, which gives percentage survival of seedlings from each treatment at the end of the first year after transplant.

It is fairly apparent from Table 9 that the most important cause of mortality throughout Trial 'b' is related to moisture and that this factor overrides other causes of mortality such as lowered temperatures related to increase in altitude and low nutrient status of soils. For instance, there is an increase in seedling mortality with gain in altitude, under shaded conditions, but in the open the reverse is true. The percent survival of seedlings under light shade is 89.2 at Rangiora, 150 feet above sea level, and at 3200 feet and 4400 feet in the Craigieburn Range it is 76.0 and 63.6 percent. In the open, however, it is only 28.1 percent at Rangiora, whereas it is 48.0 and 50.0 percent at 3200 feet and 4400 feet in the Craigieburn Range. At each altitude there is a better survival under shade than in the open but the difference becomes less pronounced with increase in altitude. The rainfall increases with the increase in altitude. Rain gauges measured by the N.Z. Forest Service show that at Rangiora it is approximately 30 inches per annum, at 3200 feet in the Craigieburn Range it is up to about 55 inches and at 4400 feet it is approximately 75 inches (C. O'Loughlin, pers. comm.). There is also a general lowering of temperature and thus a marked increase in relative

humidity. These more humid conditions at the higher levels would result in a reduction in evaporation and transpiration and in this way could cause the lower mortality rates in the open. Increase in shade would have a similar effect of reducing evaporation and transpiration and would thus explain the greater survival in each case under shaded conditions. The reduction in survival percentages under the shade with increase in altitude would result from the deleterious effect of increase in altitude, such as reduction in temperatures and decrease in length of the growing season, becoming relatively more important once the prime cause of mortality, related to moisture deficiencies, had been diminished by shading.

Under open conditions, the soil medium which gave the better percent survival of seedlings at each altitude was the subsoil with the relatively finer texture, and the soil medium which gave the lowest percent survival was the scree. Again this could be explained in terms of moisture. The clay subsoils would probably have the best moisture retaining ability as they contained the highest proportion of fine material. Even the scree soils, which represent a particularly harsh medium, gave relatively good survival percentages provided shade was applied, i.e. at 3200 feet altitude only 16.7 percent of the seedlings survived on the scree in the open but under light shade 58.9 percent survived.

Conditions which are best for survival in seedlings of Nothofagus solandri are not necessarily the best for growth. For instance, it has been mentioned that the best conditions for survival in the open are in the lighter subsoil. At each altitude, however, the total dry matter production in the lighter subsoil is inferior to that

in forest top soil (see Table 10). For instance, at the end of the second year, the forest top soil plus litter treatment in the open gave four times the total dry matter production of the treatment on the subsoil at Rangiora, seven times the dry matter production at 3200 feet in the Craigieburn Range and 12 times the dry matter production at 4400 feet in the Craigieburn Range under the same respective treatments.

The position in regard to total dry matter production between the different shade treatments is somewhat anomalous between the first year of harvest and the second year of harvest. In the first harvest, the dry matter production at each altitude was higher in the open than under light shade. This is again in contrast with survival patterns: the better survival being under light shade. In the second year, however, there was a strong tendency for growth to be better under light shade and at the high altitude site the difference was quite pronounced. This difference between the first and second years is possibly explained by nutrient deficiency resulting from break down of the litter initially incorporated in the soil media. The break down and release of nutrients would be expected to be more rapid in the open than in the shade, consequently resulting initially in the relatively more rapid growth in the open than under light shade. That deficiencies resulting from litter break down could have such a marked effect is demonstrated by a comparison between the total dry matter production figures for the soil media, forest topsoil with litter incorporated and forest top soil with coarse litter removed, at 3200 feet in the Craigieburn Range, in the open (see Table 10). In the first year, the dry matter production

Treatment			Mean Dry Weight Increase (gms)				% Total Dry Weight Increase			Mean Leaf No. Increase	Mean Plant Leaf Area Inc.(sq cm)	Mean Shoot Length Increase (in.)
Site	Shade	Soil	Root	Shoot	Leaf	Total	Root	Shoot	Leaf			
150'	1	A	.621	.680	.566	1.867	33.24	36.44	30.32	143.26	43.43	4.026
	2	A	.470	.426	.387	1.283	36.64	33.21	30.14	76.06	35.38	3.700
	1	C	.171	.050	.048	.268	63.52	18.47	18.01	18.09	3.08	0.205
L.S.D. 5%			.115	.090	.086	.256				32.68		1.131
3200'	1	A	.060	.044	.017	.120	49.79	36.22	13.99	9.55	1.47	0.445
	2	A	.063	.030	.013	.107	59.09	28.26	12.65	3.13	1.24	0.398
	3	A	.036	.017	.001	.055	65.86	31.87	2.28	- 0.04	1.23	0.221
	4	A	.023	.015	-.010	.028	82.54	53.25	-35.80	- 1.59	0.79	0.083
	1	A	.060	.044	.017	.120	49.79	36.22	13.99	9.55	1.47	0.445
	1	B	.148	.136	.085	.369	40.19	36.87	22.94	31.85	6.77	0.701
	1	C	.051	.010	-.021	.040	127.54	25.26	-52.80	- 2.80	-1.43	0.028
	1	D	.049	.017	-.018	.048	101.39	35.30	-36.70	- 0.31	- 1.07	0.126
	1	E	.025	.004	-.025	.003	848.15	148.15	-896.30	- 5.30	- 1.97	-0.146
	1	E	.025	.004	-.025	.003	848.15	148.15	-896.30	- 5.30	- 1.97	-0.146
	2	E	.049	.023	-.013	.059	82.60	39.74	-22.49	- 1.24	- 0.42	0.394
L.S.D. 5%			.028	.028	.020	.062				6.42	1.49	0.406
4400'	1	A	.054	.035	.014	.103	52.52	33.82	13.66	7.38	1.62	0.453
	2	A	.064	.018	.008	.090	71.33	20.32	8.35	1.21	1.52	0.426
	1	C	.054	.019	-.017	.055	97.58	33.84	-31.42	- 2.21	- 1.09	0.351
	1	E	.012	.008	-.025	-.005				- 5.39	- 1.86	0.126
L.S.D. 5%			.026	.011	.011	.036				3.02	1.05	0.445

Soils A, B, C, D, E as for Table 9.

Table 10A - Increases in growth for Trial 'b' at end of first year following transplant. The 150 feet altitude site is at Rangiora. The 3200 feet and 4400 feet sites are in the Craigieburn Range.

Treatment			Mean Dry Weight Increase (gms)				% Total Dry Weight Increase			Mean Leaf No. Increase	Mean Plant Leaf Area Inc. (sq cm)	Mean Shoot Length Increase (in.)
Site	Shade	Soil	Root	Shoot	Leaf	Total	Root	Shoot	Leaf			
150'	1	A	2.685	2.078	1.176	5.939	45.21	34.99	19.80	453.42	94.63	5.827
	2	A	2.664	2.087	1.545	6.295	42.31	33.14	24.54	394.76	133.33	11.044
	1	C	.520	.390	.569	1.479	35.17	26.35	38.48	160.12	33.06	2.545
L.S.D. 5%			.648	.446	.374	1.108				148.03	24.47	3.018
3200'	1	A	.254	.221	.163	.637	39.85	34.61	25.54	74.04	14.61	1.446
	2	A	.259	.184	.148	.591	43.84	31.10	25.07	48.49	14.76	1.915
	3	A	.138	.103	.087	.327	42.12	31.41	26.47	22.99	11.13	1.060
	4	A	.087	.073	.079	.238	36.61	30.45	32.94	25.55	11.93	0.835
	1	A	.254	.221	.163	.637	39.85	34.61	25.54	74.04	14.61	1.446
	1	B	.232	.294	.168	.694	33.43	42.41	24.16	93.54	15.56	1.501
	1	C	.062	.036	-.008	.090	69.64	39.55	- 9.19	2.43	- 0.73	0.619
	1	D	.033	.032	-.019	.045	73.58	71.11	-42.22	0.72	- 1.43	0.449
	*1	E	.051	.019	-.002	.068	74.88	28.08	- 2.96	9.28	- 0.36	0.315
	*1	E	.051	.019	-.002	.068	74.88	28.08	- 2.96	9.28	- 0.36	0.315
	2	E	.092	.014	-.016	.090	102.34	15.56	-17.90	- 0.50	- 0.87	0.209
L.S.D. 5%			.126	.107	.086	.291				35.14	7.20	0.934
4400'	1	A	.074	.073	.029	.176	42.38	41.34	16.28	24.38	2.79	0.552
	2	A	.175	.122	.090	.388	45.20	31.55	23.25	26.13	8.88	1.052
	1	C	.032	.010	-.027	.014	225.48	66.88	-192.36	- 5.07	- 1.72	0.370
L.S.D. 5%			.045	.033	.036	.102				12.07	3.90	0.500

* Due to the small number of replications, this treatment has not been used in the calculation of L.S.D. (see App. 7).

Table 10B - Increases in growth for Trial 'b' at end of second year following transplant. Sites are as for Table 10A.

where the coarse litter had been removed was three times that where it had been incorporated. In the second year there was little difference between the two. Presumably what has happened is that the incorporation of litter has initially resulted in a massive increase in soil organism activity. These organisms tied up much of the nutrients which should have been available for plant growth and there was thus a consequent reduction in plant dry matter production. When the break down of the litter was more or less completed the nutrients, probably largely nitrogen, again became available for plant growth, thus explaining the increased rate of growth in the forest top soil with litter relative to the forest top soil where coarse litter has been removed, in the second year.

If the cause of the relative difference between the first and second year dry matter production in the open and under light shade was in fact related to nutrient availability in the way described in the last paragraph, then it would be expected that the second year harvest would be the most indicative of the shade conditions most suitable for dry matter production, and it could be assumed, therefore, that light shade results in a greater dry matter production than open conditions. Field observations would certainly suggest that this is in fact the case. The photosynthetic efficiency of the seedlings, though, as measured by total dry matter production per unit of leaf area, is with the exception of the 4400 feet altitude site in the second season, better in the open than under any of the shades. The total dry matter production over the two years, per square cm. of leaf area was 0.119 gms. in the open at 150 feet altitude but only 0.091 gms. under light shade. At 4400 feet it was 0.064 gms. in the open

and 0.057 gms. under light shade but at 4400 feet it was 0.040 gms. in the open but 0.059 gms. under light shade. It would require further studies to establish how general this reversal in net assimilation rates at the higher altitudes was, but studies on height growth of saplings discussed later in Section 4.3.2. suggest a similar interaction of shade and altitude. The different shade requirements for total dry matter production and for peak photosynthetic efficiency in the second year results from a reduction in the mean leaf area per plant between the light shade and the open. At the end of the second year the total leaf area per plant at the 150 feet altitude site was 97.42 sq. cm. in the open but 136.14 sq. cm. under light shade. At 3200 feet it was 17.28 sq. cm. in the open and 17.49 sq. cm. under light shade and at the 4400 feet site it was 5.63 sq. cm. in the open and 11.37 sq. cm. under light shade (see App. 8). However, there was little change in leaf number between the two shade treatments at any of the three altitudes. This reduction in leaf area, through reducing the leaf size, serves to reduce the transpiring surface of the plant under full light conditions. Certainly the mortality figures for this trial suggest that Nothofagus solandri is very drought prone in the seedling stage. The lower total dry matter production in the open would thus result from inefficiency in transpiration rather than from inefficiency in photosynthesis.

Under the heavy shade treatments, shade 3 and shade 4, the photosynthetic efficiency of the seedlings continues to deteriorate as does the total plant dry matter production. At 3200 feet the net assimilation rates for the four shade treatments grade from 0.065 in

the open to 0.023 gms. per square cm. under shade 4. At the same altitude the total dry matter production under shade 4 over the two years is only a third of that in the open. The increase in leaf numbers is likewise reduced to about a third. However, this is compensated by an increase in the mean leaf size and consequently the leaf area per seedling is not greatly reduced. The production of this leaf area utilizes a great deal less plant material under the shade than in the open, i.e. under shade treatment 4 the leaf weight increase to give an 11.93 sq. cm. leaf area increase is only 0.079 gms. while in the open it requires an increase of 0.163 gms. to give 14.61 sq. cm. of leaf area.

As would be expected, the seedlings show a marked decrease on total dry matter production with increase in altitude. For instance, in forest top soil, under full light, the mean total dry matter production over the two year period was 5.939 gms. at 190 feet altitude, 0.637 gms at 3200 feet and 0.176 gms at 4400 feet. Paralleling this decrease in total dry matter production with increase in altitude is a decrease in the net photosynthetic efficiency of the seedlings growing in the open. This decrease in net assimilation rate is probably related to a shorter season for growth and to lower mean temperatures.

When seedlings of Nothofagus solandri are grown on soils such as subsoil and scree which are low in available nutrients, they are able to direct most of their growth into the root system at the expense of the leaves (see Table 10). Under such conditions the root system is very fibrous when compared with the root system of seedlings growing on better soil. Apparently this is an attempt by the seed-

ling to exploit the maximum volume of soil with the small increases in growth which take place under such situations. The ability of Nothofagus solandri to survive and grow naturally on poor soils in areas of high rainfall may well be related to this ability of the plant to concentrate nearly all of its growth into the root system.

4.2.6. Vegetative reproduction

Sometimes on steep slopes towards the bushline, the trunks of mountain beech run downhill for ten feet or so before gradually ascending to an erect position. The canopy height where this occurs is generally less than twenty feet. According to P. Wardle, 1963, this habit originates when the saplings are weighed down by drifting and avalanching snow. This is the situation where layering can and does occur (see Fig. 26). Small, whippy branches are held in contact with the soil by weight of snow on the foliage. At the point of contact callus formation takes place and subsequently roots may develop.

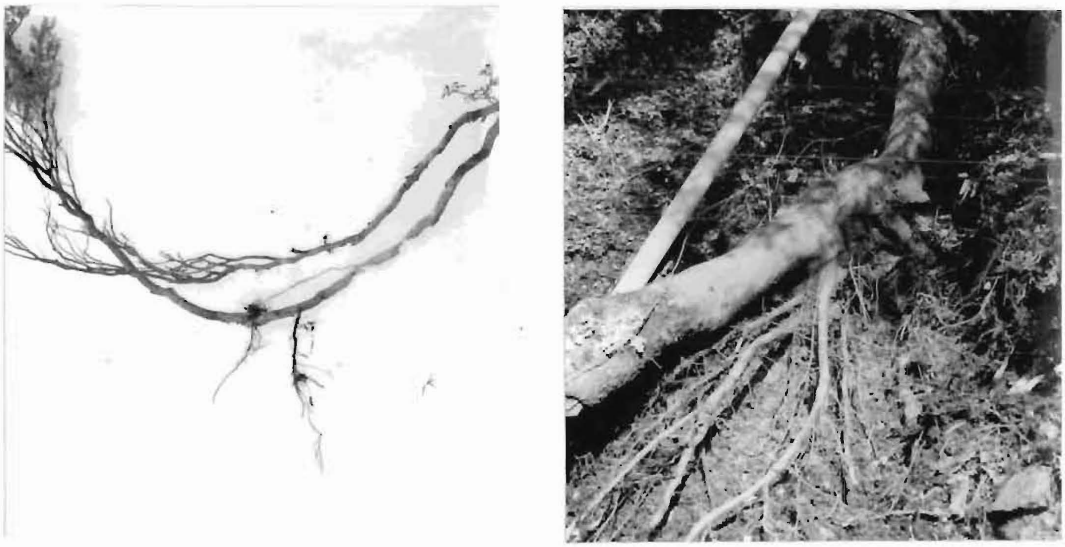

Fig. 26 - Layering in mountain beech at 4200 feet altitude in the Travers Valley, Lake Rotoiti, North-west Nelson.

4.2.7. Summary and Conclusions

Flowering in Nothofagus solandri occurs some time between October and mid December. The species is monoecious but the staminate and pistillate flowers are borne on the same vegetative shoots. The flower primordia are formed during the summer previous to that in which flowering takes place. There is a marked variation in the extent of flowering between seasons but sometimes, at low altitude, trees may flower twice in one season. Seedlings as young as six years of age have been known to flower but there is no evidence for viable seed being produced until the trees are 25 or 30 years of age.

Abundant flowering does not necessarily result in abundant seeding due to the possible intervention of unfavourable climatic conditions and there is a marked tendency to periodicity in seeding. Good seed years occur at approximately ten year intervals but between the good seed years there may be several partial seed years. A good seed year may produce up to 1000 times more seed than a poor seed year and in a good year there may be as many as 53 million seed produced per acre. This represents 470 lbs of seed. A good seed year may occur throughout most of the Nothofagus solandri forests in the country but it is not necessarily country wide and the Canterbury foothills and low altitude Southland forests seem to have a different pattern of seed years to the Main Divide forests. Seed quality is much better in a good seed year than in a poor one. In a good year up to 57 per cent of the seed shed may be sound while in a poor year there may be no sound seed at all. Seedfall occurs between March and May and tends to occur earlier in poor seed years than in good seed years. The quality of the seed varies throughout seedfall

season. Early and late in the season there is a lower percent of sound seed than towards the centre of the season.

Wind is the main agent of seed dispersal in Nothofagus solandri. There is a suggestion that water dispersal may be important under certain circumstances. Normal dispersal of the seed may take place up to at least ten times tree height away from the parent tree though in grassland seedlings of the species are seldom found further than tree height distant.

Germination can occur at low altitudes in the North Island two to three months after the seed is shed but in general the seed overwinters on the ground and begins to germinate in the following spring between the months of September and December. It seems that the time of initial germination can be fairly closely correlated with soil temperatures and occurs when the four inch soil temperatures as measured between 9 a.m. and 10 a.m. consistently rise above 44 or 45°C. Once the first seedlings have appeared germination usually proceeds fairly rapidly. The seedlings appear to be particularly susceptible to death by desiccation during the initial stages of germination. Under warm moist conditions, it takes about ten days after the seed is sown for the radical to appear and about a month before the cotyledons emerge from the seed coat. It is about two weeks later before the first foliage leaves appear. There is thus a period of about two months during which the seedling must be fairly susceptible to adverse conditions. The greatest rate of mortality in the first season seedlings occurs in the summer months following germination. Over these months 80 per cent or more of the seedlings may die. The rate of mortality is greatly reduced during the following winter

months and thus it appears that the young seedlings are much more susceptible to the summer fluctuations in soil moisture than to the low temperatures of the winter months.

Older seedlings of Nothofagus solandri can persist under the shade of the parent canopy for long periods without making much effective growth. The mean growth rates of these 'advance growth' seedlings can be as low as 0.06 inches per annum. On the other hand seedlings of similar size can grow 18 inches per year provided there is adequate light. Even though growth may be so slow, mortality rates of these seedlings are not high, and appear to be in the vicinity of about 8 percent per year. Even these older seedlings perform poorly under dry conditions. Their photosynthetic efficiency is probably best under full light except perhaps near the bushline but under full light conditions the potential growth rates are not achieved as the total plant leaf area is considerably reduced, probably in an attempt to reduce transpiration. In fact the maximum dry matter production tends to be under light shade. When seedlings of Nothofagus solandri are grown under dense shade they are able to in part compensate for the low light conditions by producing large leaves which have up to $2\frac{1}{2}$ times the leaf area of leaves of open grown plants. The weight of plant material utilised in producing unit leaf area is much less in the shade than in the open. When growing on poor soils, the survival rate of Nothofagus solandri seedlings may be quite high provided there is adequate moisture, even though there may be very poor growth. Most of the growth which does occur is directed into the fibrous root system.

Increase in altitude delays the time of flowering by almost one

month per 1000 feet. On the other hand the time of seed fall, even in a good seed year may be hardly delayed at all, and there can be about three months less time for the seed to develop and ripen near bushline, than at the lower levels. Seed weight is reduced towards the bushline, possibly as a result of this reduction in the time interval between flowering and seeding and possibly for the same reason the seed quality falls off markedly towards the upper limits of the species. Seed quality seems to be little affected by deterioration of site quality at any one altitude, but the quantity of seed shed is reduced, both by increase in altitude and by deterioration of site quality at the one altitude. The percent germination of sound seed is much lower near the bushline than lower down. This is possibly due to a shortening of the period over which temperatures are adequate for germination to occur. Changes in altitude also influence the rate of mortality of seedlings during the first summer and the stage of development reached in the first year and near the bushline seedlings may only reach a 2 foliage leaf stage in their first growing season. There is a reduction of both the net assimilation rate and the total dry matter production of older seedlings with increase in altitude but mortality rates are not greatly different. There tends to be lower mortality rates in the open at the higher altitudes as a result of improved moisture conditions, but a higher mortality rate under shade.

4.3 TREE GROWTH AND MORTALITY

4.3.1. Phenology

In order to study the seasonal pattern of growth in Nothofagus

solandri, between nine and twelve open growing saplings, each between six and ten feet high, were selected during early spring 1967 at each of five different sites. The sites chosen were at 4400 feet, 3900 feet, 3200 feet and 1700 feet in the Craigieburn Range and at 150 feet altitude at Rangiora. On each sapling one lateral shoot at about three feet above ground level, and the terminal shoot were marked. From the start of bud elongation throughout the growing season, measurements of the growth were made at about weekly intervals on each of the marked shoots. The time of initial bud movement, bud burst and growth cessation was noted and the total growth put on by each terminal and each lateral for the growing season was measured. The cumulative percentage of total annual growth which had occurred up to the date of each measurement was calculated, and the mean cumulative percentage for each site is given in Appendix 9. During the season a number of the marked shoots became broken or died back and in such cases all measurements were discarded. The final number of saplings used in the calculation of terminal and lateral growth at each site is also given in Appendix 9.

The seed trays described in Section 4.2.2. were used to study leaf and twig fall. The site of each line of seed trays is summarised in Table 3. Litter was collected from the canisters at the bottom of each seed tray at approximately monthly intervals from April 1965 until March 1968 in the Craigieburn and Kaweka lines and from April 1966 to March 1968 in the Mt Thomas line. Each collection was sorted into leaves and twigs which were oven dried at 95°C, and then weighed. The mean leaf and twig fall for each line of trays for each period between collection was calculated and corrected to produce

monthly fall figures using an assumption that the fall was regular throughout each period. This correction had to be made as the time of collection did not always coincide with the last day of the month. The corrected mean monthly fall for each line of trays was converted to lbs per acre and these figures are given in Appendix 10.

The buds of Nothofagus solandri open sometime between late September and early December. Prior to burst, the buds go through a period of elongation which may proceed over two months before bud burst actually takes place. During this period, cold temperatures may temporarily halt bud elongation and during the present study heavy snowfalls in the Craigieburn Range during the first three weeks of November actually stopped elongation for up to one month (see Figs. 27 and 28). Once temperatures rose, elongation and subsequent bud burst proceeded and the buds apparently suffered no damage from the unseasonably low temperature conditions.

The date of opening of buds is apparently delayed with increase in altitude. P. Wardle, (1963), measured a 2 month delay in the time of bud burst during the 1958/59 and 1959/60 growing seasons between Rangiora at 150 ft and the Craigieburn Range at 4500 ft altitude. The present study, for the 1967/68 growing season showed a similar delay. The early pattern was slightly complicated due to the unseasonal November snowfall but 10 percent of the seasonal growth on the terminals at Rangiora had occurred by the end of the first week in November, whereas at 4400 feet in the Craigieburn Range it had not occurred until 5 to 6 weeks later (see Fig. 27). On the lateral shoots there was almost a 2 month delay (see Fig. 28).

The time of bud opening also varied from season to season, and

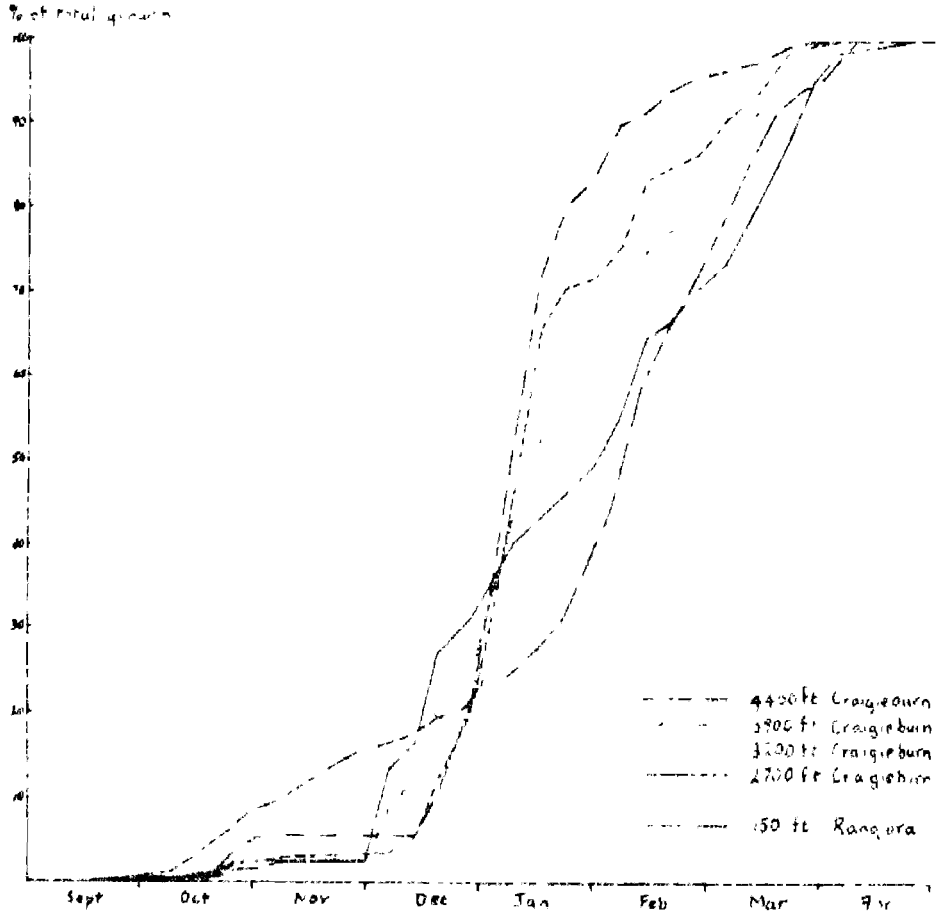

Fig. 27 - Cumulative mean percent of total annual growth on terminal shoots throughout the 1967/1968 growing season at a number of altitudes in the Craigieburn Range and at Rangiora.

was approximately one month later during the 1967/68 season that for corresponding altitudes during the 1958/59 and 1959/60 seasons. P. Wardle (loc. cit.) states that topography also has a considerable influence on the time of commencement of growth and uses the example that trees bordering a frost hollow opened their buds a month later than trees on adjacent warm slopes. He also suggests that growth begins later in wet cloudy districts than at similar elevations in drier, sunnier districts.

There is some growth on both the terminal and the lateral shoots at all altitudes until about the end of March but, whereas on

the terminals the eighty percent of the total annual growth which occurs during the height of the growing season is spread over 1½ months at 4400 feet, the same percentage of growth is spread over increasingly longer periods with decrease in altitude until at 150 feet altitude it takes 4½ months (see Fig. 27). There is the same pattern with the laterals but the difference between altitudes tends to be less pronounced (see Fig. 28).

P. Wardle, (1963), mentions that the annual cycle of growth in Nothofagus solandri is complicated by the presence of two different kinds of shoots. He states that virtually all shoots of adult plants

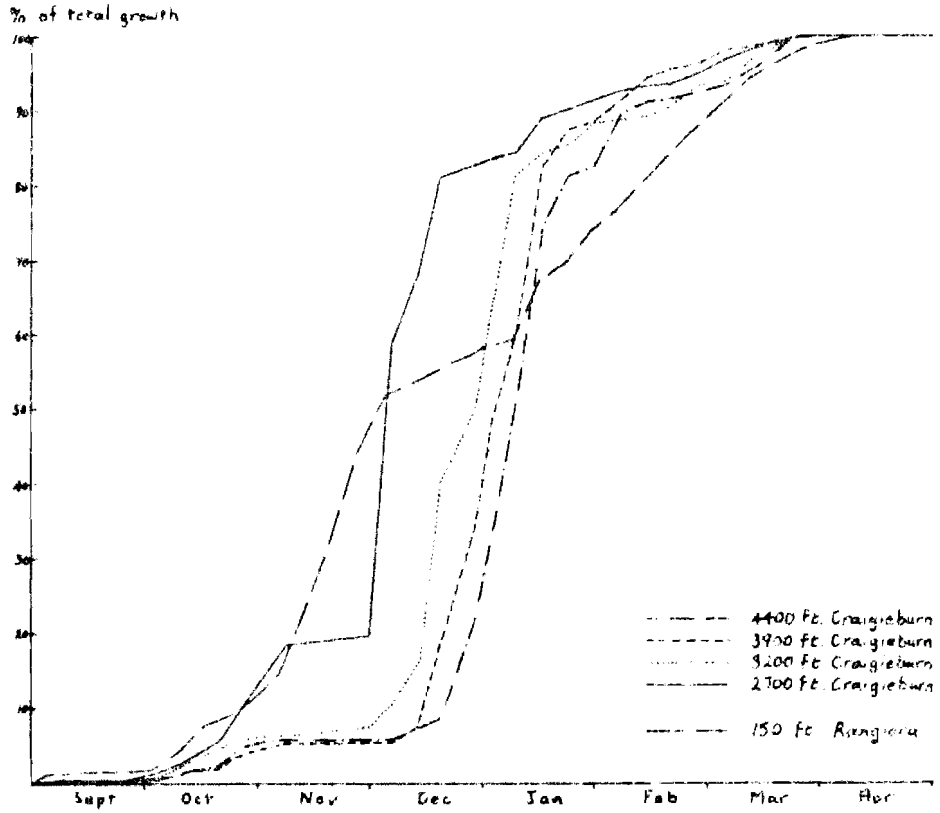

Fig. 28 - Cumulative mean percent of total annual growth on lateral shoots throughout the 1967/1968 growing season at a number of altitudes in the Craigieburn Range and at Rangiora.

and the majority of shoots of young plants expand the leaves already present in the overwintering bud during a rapid flush of growth which ends in the formation of new buds. These he refers to as limited growth shoots. The leading shoots of seedlings and saplings on the other hand, produce new leaves continuously through the summer and often lower axillary buds formed in the earlier part of the summer open later in the same summer to produce lateral shoots. Bussel, (1968), carried out further measurements which more or less confirm P. Wardle's findings. He records that in species of Nothofagus, seedlings over one year of age and young trees produce two or three series of leaves in a year, whereas in seedlings in their first year and in adult trees the growth is continuous. He also concludes that whereas the flushes of individual seedlings are not in step, those of young trees are, there being one flush in the spring and one in the autumn.

The present study showed that the number of flushes in growth in saplings is fairly closely related to the altitude. Thus at 4400 feet both terminal and lateral shoots on all saplings measured had only one flush of growth. At 3900 feet, all laterals and nine out of the ten terminals had one flush of growth but the remaining terminal had two flushes. At 3200 feet, all the laterals still had one flush of growth but seven out of the ten terminals measured had two. At 2700 feet the lateral shoots showed one flush only but four out of the ten terminals had three flushes and the remaining six had two flushes, and at 150 feet, at Rangiora, four out of the nine lateral shoots had two flushes. The remainder had one and in the terminal shoots three had three flushes and three had two flushes.

After the first flush of growth a new bud tends to be formed but where there are three flushes the interval between the second and third flush is a slowing down of growth rather than a definite cessation. At Rangiora the flushes tend to be synchronous as suggested by Bussel, (1968), but at the higher altitudes the second and third flushes are not necessarily in step from sapling to sapling.

There is a time lag between bud burst in seedlings and bud burst in the adult tree. According to Bussel there is about a three week delay. During the present study it was noted that bud burst on the marked lateral shoots preceded bud burst on the terminal shoots by up to two weeks.

The leaves of Nothofagus solandri are generally shed during the growing season following the one when they are produced. P. Wardle (1963) mentions that in slower growing shoots they may be retained for two years. The proportion of leaves which are retained for two years is negligible and can be virtually discounted. Both Wardle and Bussel maintain that leaf fall peaks occur during the earlier part of the growing season just following bud break but the present study indicates that this is not entirely so and that the peak is usually prolonged for the length of the growing season (see Fig. 29). At Mt Thomas, and to a slight degree at the lower altitude sites in the Kaweka and Craigieburn Ranges, there was some tapering off of leaf fall during the growing season but at the higher altitudes in both the Kaweka and Craigieburn Ranges leaf fall was virtually straight linear from the beginning of December through until the end of April. During this five month period 75 to 80 per cent of the leaf fall occurred in all but the Mt Thomas line of trays.

At all sites there was negligible leaf fall during August and September.

The time of peak leaf fall is delayed with increase in altitude. This is apparent from Fig. 29. The delay is about two months between 1700 feet at Mt Thomas and 4400 feet in the Craigieburn Range, and about two to three weeks between 3400 feet and 4400 feet in the Kaweka Range. There was also a mean delay, over the three years during which the study took place, of about two weeks, from the Kaweka Range to corresponding altitudes in the Craigieburn Range. The pattern of leaf fall may also vary from year to year. Over the three years of the study, onset of the peak leaf fall showed a variation of up to one month (see Appendix 10A).

Twig fall also tends to be deciduous though not to the same marked degree as leaf fall (see Fig. 30). The tendency is not as pronounced at lower altitudes as at higher altitudes. The peak of twig fall is from December through until April which is the same time as peak leaf fall and again, as for leaf fall, the twig fall is least in August and September.

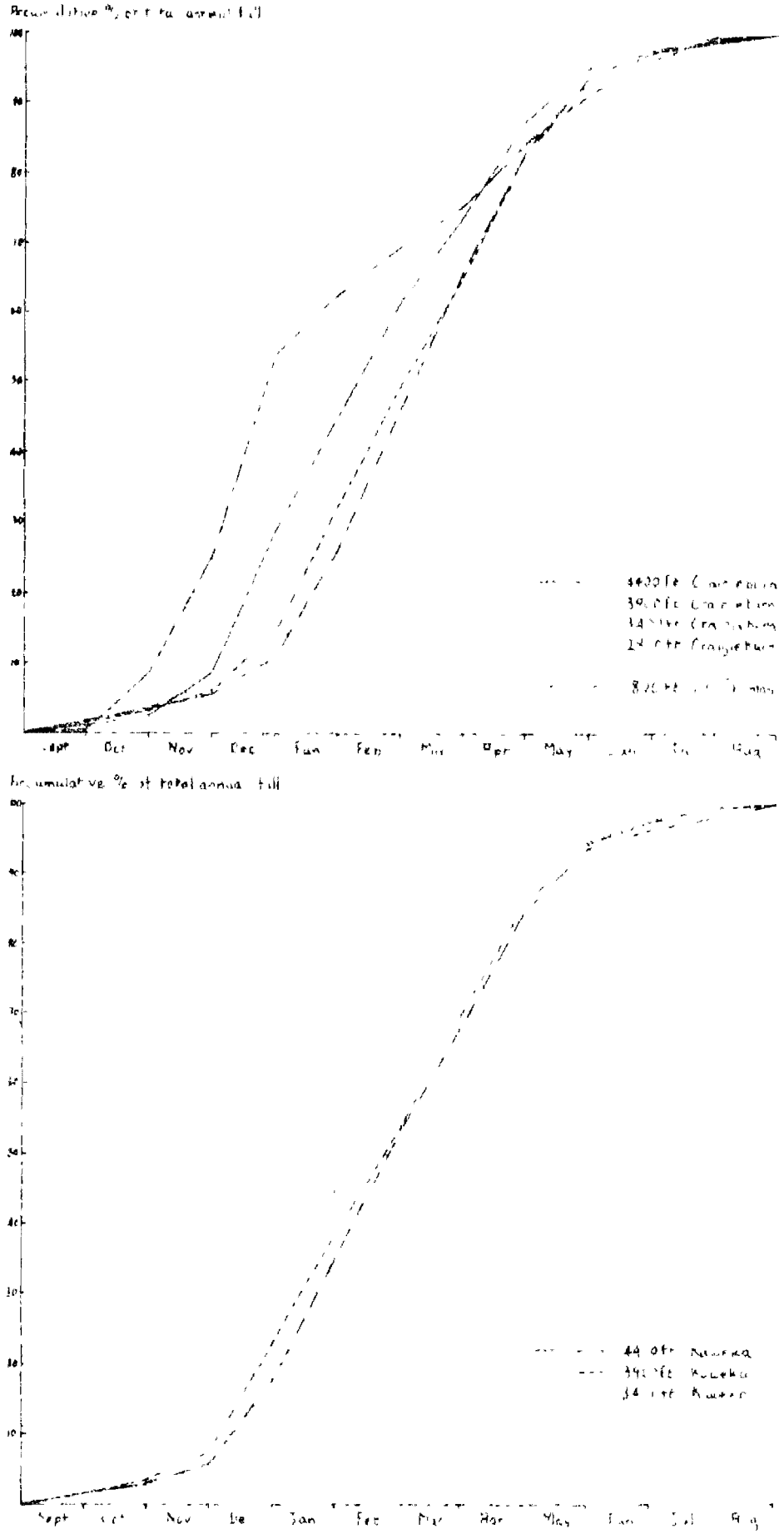

Fig. 29 - Progress of leaf fall for a number of sites in the Kaweka and Craigieburn Ranges and at Mt Thomas. The graphs for the Kaweka and Craigieburn Ranges represent the means of three years whereas that for Mt Thomas represents the mean of two years of collection.

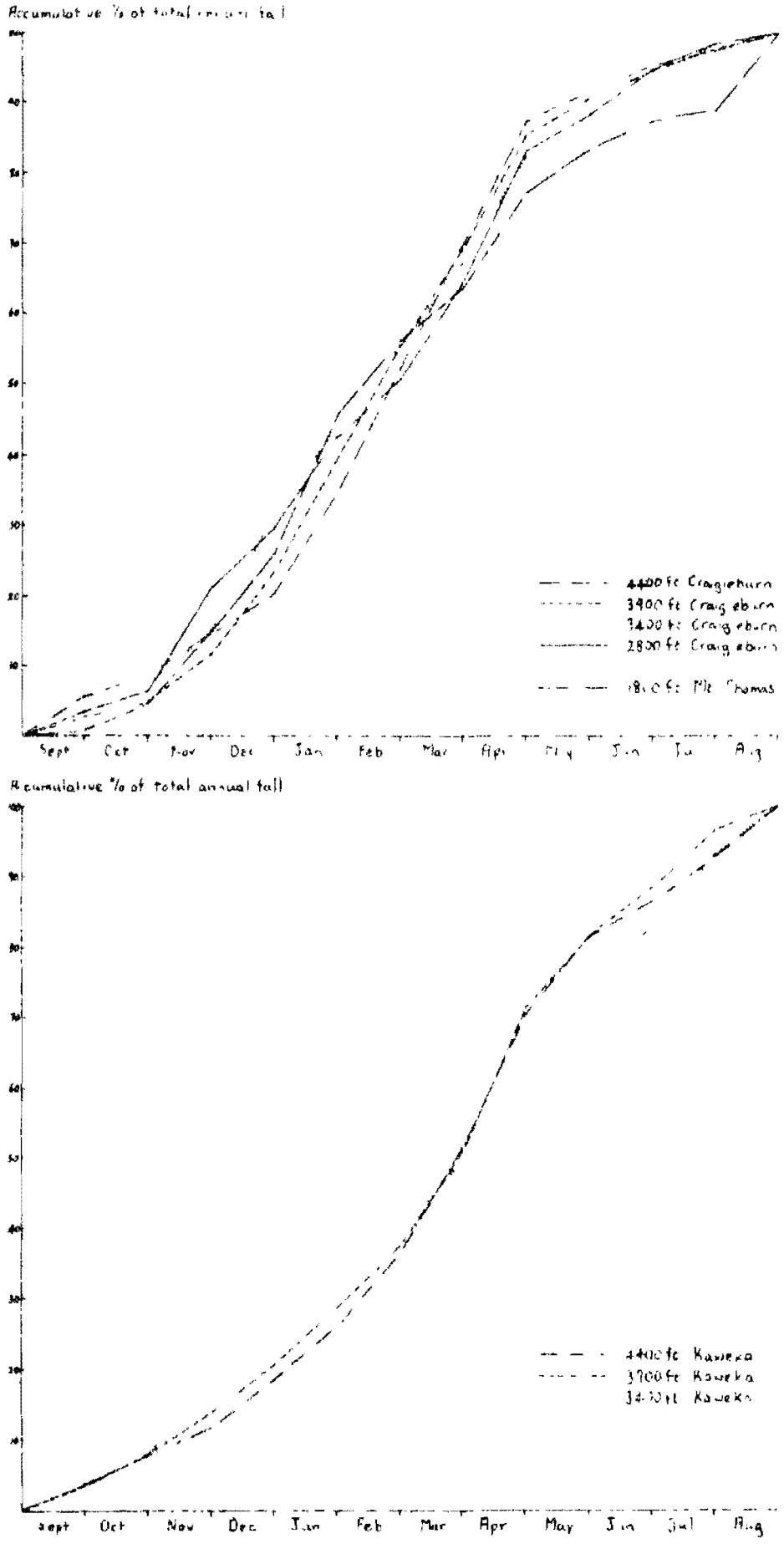

Fig. 30 - Progress of twig fall for a number of sites in the Kaweka and Craigieburn Ranges and at Mt Thomas. The graphs for the Kaweka and Craigieburn Ranges represent the means of three years whereas that for Mt Thomas represents the mean of two years of collection.

4.3.2. Height growth

Data from the phenology measurements described in the last section were also used for calculation of total annual extension for both the terminal and lateral shoots of saplings in the Craigieburn Range and at Rangiora. The results are given in Table 11. The saplings used in the study, though providing an indication of the order of magnitude of annual growth in the open at a number of different altitudes, give no idea of the pattern of growth throughout the life of the trees. Neither do they give any indication of the annual height increment on saplings growing in stands. For this information stem analyses were used. Ten trees with diameters at breast height ranging from 4 inches to 20 inches were selected from within a stand of 'Association D 1' mountain beech at 3200 feet altitude in the Craigieburn Range. A further ten trees from within a similar diameter range were selected from the same area and the same association but at 4400 feet altitude. These trees were felled and discs were taken from each at ground level and at 10 feet intervals up the trunk until the top of each tree was reached. In each case an extra disc was removed from breast height, i.e. 4 feet 6 inches above ground level. The total age of each tree was determined by counting the annual growth rings on the basal disc, and the number of years required by the tree to reach the height from which each of the upper discs had been removed was calculated by subtracting the number of growth rings on each of the discs from the total age of the tree. The mean number of years for a tree to reach 4 feet 6 inches, 10 feet, 20 feet, 30 feet, etc, under competing stand conditions was subsequently calculated for each of the two altitudes

Site	Terminal (in.)			Lateral (in.)			Ratio Terminal/Lateral		
Altitude	No. of Saplings	Mean Inc.	S.E. P = 0.05	No. of Saplings	Mean Inc.	S.E. P = 0.05	No. of Saplings	Mean Inc.	S.E. P = 0.05
Rangiora									
150 feet	6	8.62	6.78	6	5.77	6.73	6	3.33	3.39
Craigieburn									
2700 feet	10	15.93	2.94	12	2.29	0.50	10	7.34	1.70
3200 feet	10	8.09	2.40	12	1.62	0.50	10	5.99	2.73
3900 feet	10	5.64	1.65	12	2.32	0.68	10	2.87	1.11
4400 feet	10	1.94	0.86	9	1.53	0.65	9	1.41	0.55

Table 11 - Mean total annual extension on the terminal and one lateral shoot from a number of saplings at each of a number of altitudes in the Craigieburn Range and at Rangiora.

and the results are shown in Fig. 31 and Appendix 11.

The maximum annual terminal growth measured during the present study was 23.7 inches. This was on one of the open grown saplings from 2700 feet in the Craigieburn Range. The terminal growth rate of the open grown saplings from the sites in the Craigieburn Range show considerable variation between altitudes (see Table 11). The mean terminal growth at 2700 feet is 15.93 inches while at 4400 feet it is 1.94 inches, or less than one eighth of that at the lower altitude. The mean lateral growth rate does not vary a great deal though, and as a result the apparent importance of apical dominance of the sapling decreases markedly with increase in altitude. Terminal growth is only 1.4 times lateral growth at 4400 feet but at 2700 feet it is 7.3 times greater. This change in the terminal growth to lateral growth ratio would account for the change in growth form of open grown Nothofagus solandri from a short squat, often semi-prostrate tree near the bushline, to a tall tree at lower altitudes.

Even though there is a reduction in the terminal growth and in the ratio of terminal growth to lateral growth with increase in altitude in the Craigieburn Range, the same relation does not extend down to the saplings measured at Rangiora. Height growth at Rangiora is very variable. In sheltered places, saplings can put on up to 36 inches of height growth in a year, but where exposed they suffer from frequent die-back of the terminal shoot and the ratio of terminal to lateral growth again tends to be reduced. The variation is probably related to the low rainfall and frequent dry winds of Rangiora which lies outside the present natural distribution of Nothofagus solandri.

Whereas increase in altitude results in a considerable reduction in terminal growth on open grown saplings, those growing in the competition of a dense stand do not appear to be greatly influenced in this way. The stem analyses gave a mean increment on saplings up to 10 feet high of approximately 3 inches per year, both at 3000 feet and at 4400 feet altitude (see Fig. 31 and App. 11). The mean annual increment is similar on saplings up to 20 feet high between the two altitudes but beyond this there is a rapid reduction of height growth rates at the higher altitude, and the ultimate height of the trees at 4400 feet is only about 45 feet as compared with 75 feet at 3000 feet altitude.

Fig. 31 - Age plotted against specific tree heights. Each curve represents the mean of ten stem analyses.

The pattern of height growth throughout the life of the trees follows the normal sigmoid pattern, with initial slow growth and then a period of rapid growth while the tree is in the sapling stage, and then a slowing down as the height of the surrounding stand is approached. At both altitudes the mean tree reached half its total height by 80 to 90 years of age and by 150 years was approaching maximum height. From then until the tree dies an increasing proportion of the growth effort becomes involved in crown extension and less in height increase.

The ultimate height attained by stands of Nothofagus solandri depends on the site and is thus related to the associations defined in Section 3. Under extreme conditions of poor soil development the species may only grow to 1 foot 6 inches high while stands over 80 feet high may be encountered where the soil is deeper and presumably more fertile and where the altitude and rainfall are suitable.

It would be expected that just as the stand top height may vary from one Nothofagus solandri association to another (see Section 3) so may the mean height increment. Unfortunately, other than for Association D 1 there are few measurements.

4.3.3. Diameter growth

The pattern of diameter growth of Nothofagus solandri was studied on discs taken from the twenty trees which had been felled for stem analysis in the Craigieburn Range. As mentioned in the previous section, ten of these trees were selected from a stand at 4400 feet altitude and the remainder from a stand at 3000 feet. The disc selected for measurement from each tree was the one which had been removed from 4 feet 6 inches up the trunk. On each disc,

radii representing the uphill, downhill and two sides of the tree facing the contour direction, were marked from the core of the disc to its circumference. Measurements were taken along each radius to the points where they intercepted the growth rings which represented each ten years of the tree's age. The mean distance from the core to each such growth ring was then calculated for each tree and then for all trees at each of the two altitudes. The results are given in Appendix 12 and are shown graphically in Fig. 32.

A number of stands were selected from each of seven of the Nothofagus solandri associations (see Section 3). These stands were chosen from the Kaweka Range, Mt Ruapehu, Buller River headwaters, Grey River headwaters, Paparoa Range, Craigieburn Range, Hump Range and Spey River, Fiordland. From each a number of trees were systematically selected and from each of these four increment cores were taken around the trunk at breast height. The number of growth rings visible on the outside inch of wood on each increment core were counted and averaged for each tree. The mean number of rings per inch was then calculated for each association and these are presented in Table 12.

As can be seen in Fig. 32 the diameter growth at breast height is virtually straight linear throughout the life of the tree. The slowing down of diameter growth normally encountered in tree species as maturity is approached is not apparent in this study on Nothofagus solandri. It is probable that it is restricted to a short period just prior to death. The graphs also suggest that there is little difference between the rate of diameter growth at the 3000 feet altitude site and near the bushline at the 4400 feet site. The mean

number of rings per inch of disc radius for the ten trees at 3000 feet altitude is 27.06 $\pm$ 3.25 (P = 0.05) while at 4400 feet it is 24.10 $\pm$ 2.55. This retention of the rate of diameter growth with increase in altitude is not an isolated phenomenon. Increments taken in the Harper branch of the Rakaia catchment show a similar pattern. Here at 3100 feet altitude the mean number of rings per inch at breast height on sample trees was 29.37 $\pm$ 3.30 (P = 0.05). At 3600 feet it was 28.87 $\pm$ 3.57 while at 4000 feet it was still only 30.95 $\pm$ 3.89. Increment cores taken in the Kaweka Range and at Ruapehu show a similar pattern.

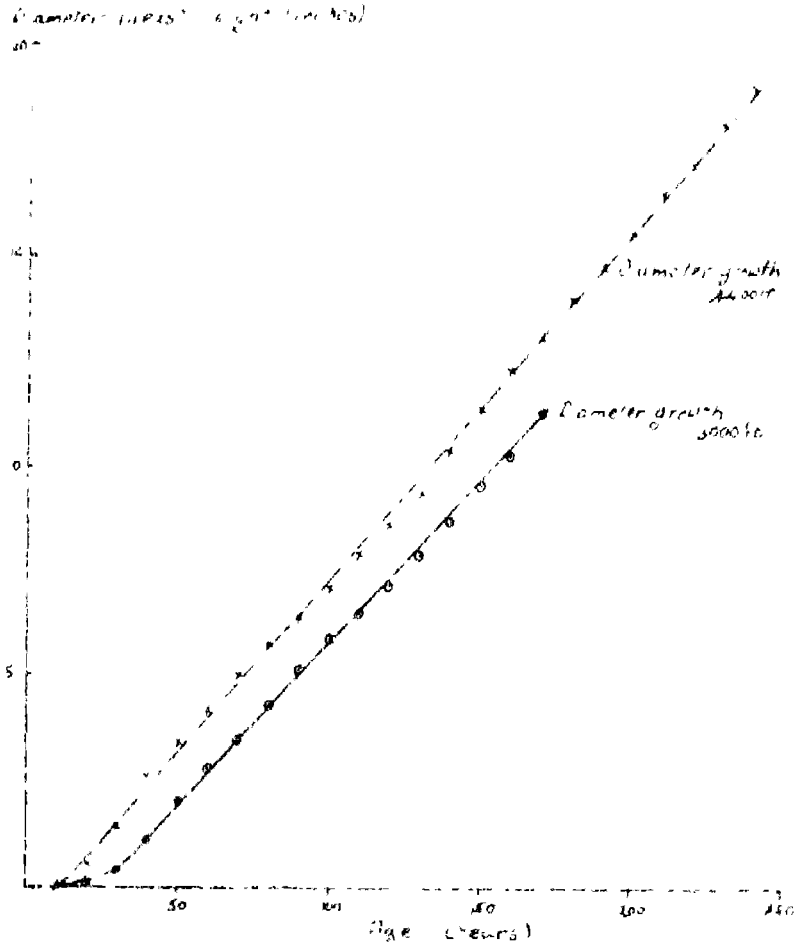

Fig. 32 - Diameter under bark at breast height plotted against tree age at Craigieburn Range (Association D 1). Each graph represents the mean values for ten trees.

Association	No. Stands Sampled	No. Trees Sampled	Mean No. rings/inch	S.E. P = 0.05
A 1	2	20	118.10	10.95
B 2	7	128	60.12	3.69
B 3	4	48	60.89	5.33
C 5	2	23	23.32	5.09
C 6	7	69	27.41	2.16
D 1	7	126	29.41	1.40
D 4	2	18	43.72	7.12

Table 12 - Diameter growth rates of Nothofagus solandri in a number of different associations.

Though there appears to be little change in the breast height diameter growth with change in altitude within a Nothofagus solandri association, there may be quite large differences in growth rates between associations. This is apparent from Table 12. Of the seven associations sampled in this study, C 5 gave the fastest mean growth rate with only 23.32 rings per inch of radius. A 1 on the other hand gave the slowest growth with 118.10 rings per inch. The most rapid diameter growth measured in the present study was at a low altitude site in Southland where one tree had 8.5 rings per inch (see Fig. 33). The slowest growth on the other hand was from a stunted tree of Nothofagus solandri on a high altitude, slow weathering rock surface in Western Fiordland where the rate was 179.0 rings to the inch. The diameter growth rates quoted above are all for trees from within stands. Wardle (1963) suggests that trees of Nothofagus solandri marginal to a stand can have rings up to 0.5 cm

in diameter. (This is equivalent to about 5 rings to the inch).

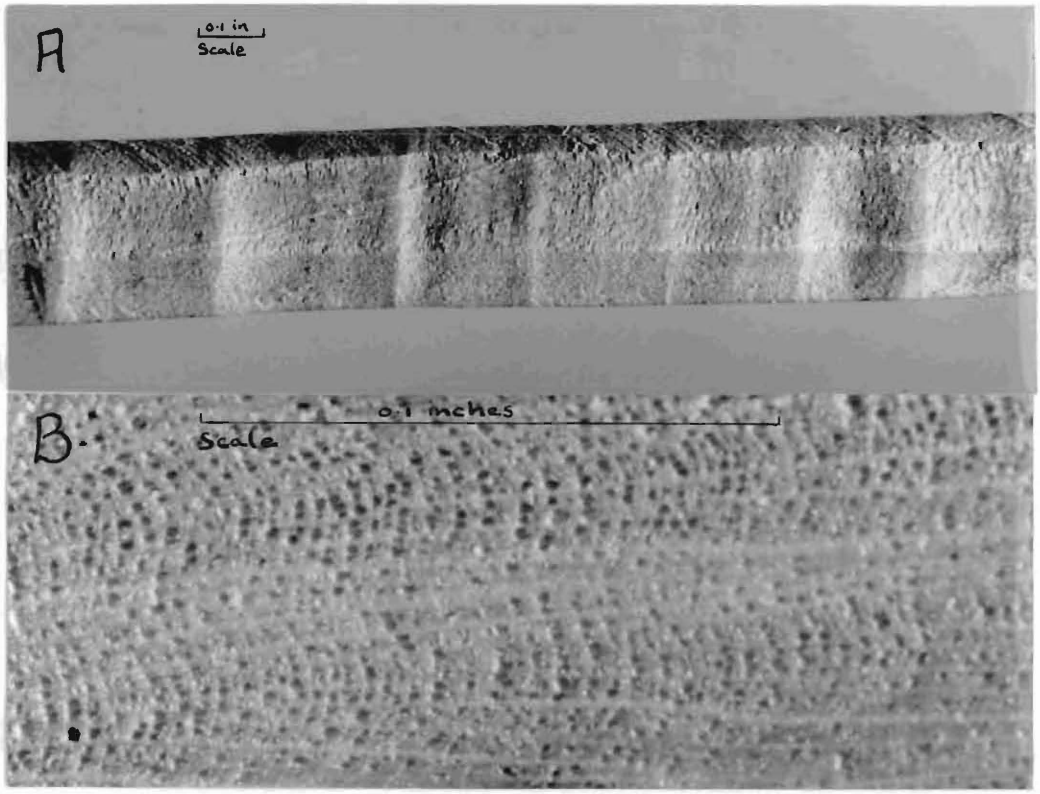

Fig. 33 - Extremes of diameter growth in Nothofagus solandri.
Sample A is from low altitude Southland forest (Association C 5).
Sample B is from a high altitude Western Fiordland forest (Association A 1).

The large variation in rates of diameter growth encountered in this study on Nothofagus solandri demonstrates the necessity for adequate site descriptions to be given where growth rates of a species are quoted.

4.3.4. Volume growth

The same twenty trees from the Craigieburn Range which were used in the studies on the pattern of height and diameter growth were

also used to calculate volume growth. The diameter for each tenth year of each tree's life was measured from the annual growth rings which were taken at ten feet intervals up the stem. The main trunk volume at the end of each ten year period was then calculated for each tree by the use of Smalian's formulae (see Husch, 1963). The mean pattern of volume growth of the main trunk was then calculated for the 3000 feet and for the 4400 feet site. These results are given in Appendix 13 and are shown graphically in Figure 34.

The 'Harmonised Curve' method which is adequately described in most text books on forest mensuration (see Husch, 1963), was used to produce a two way volume table for Nothofagus solandri showing total main stem volume under bark against ~~age~~ diameter under bark and height. The total main stem volume data at the end of each successive ten year period throughout the life of each of the twenty trees studied, served as independent samples in the calculation of this volume table which is presented in Appendix 14.

The straight linear relationship between diameter at breast height and age, described in the last sub-section, must mean that the basal area increment is developed at an increasing rate throughout most of the life of the tree since, as the diameter of the tree increases, new growth, is being put onto an increasingly greater circumference. Likewise volume increases would be expected to become progressively greater with age and this in fact appears to be so (see Fig. 34). The volume increment for the first 50 years is negligible and the periodic mean annual increment per tree over this period is less than 0.02 cubic feet. In the next 50 years it climbs to 0.09 cubic feet per year. Up to this age little difference

is apparent between the increments at 3000 feet and 4400 feet altitude but with increase in age over 100 years the volume increment becomes much greater at the lower altitude site. From 100 to 150 years of age at 3000 feet, the periodic mean annual increment is 0.2 cubic feet per year, while from 150 to 200 years of age it is over half a cubic foot per year.

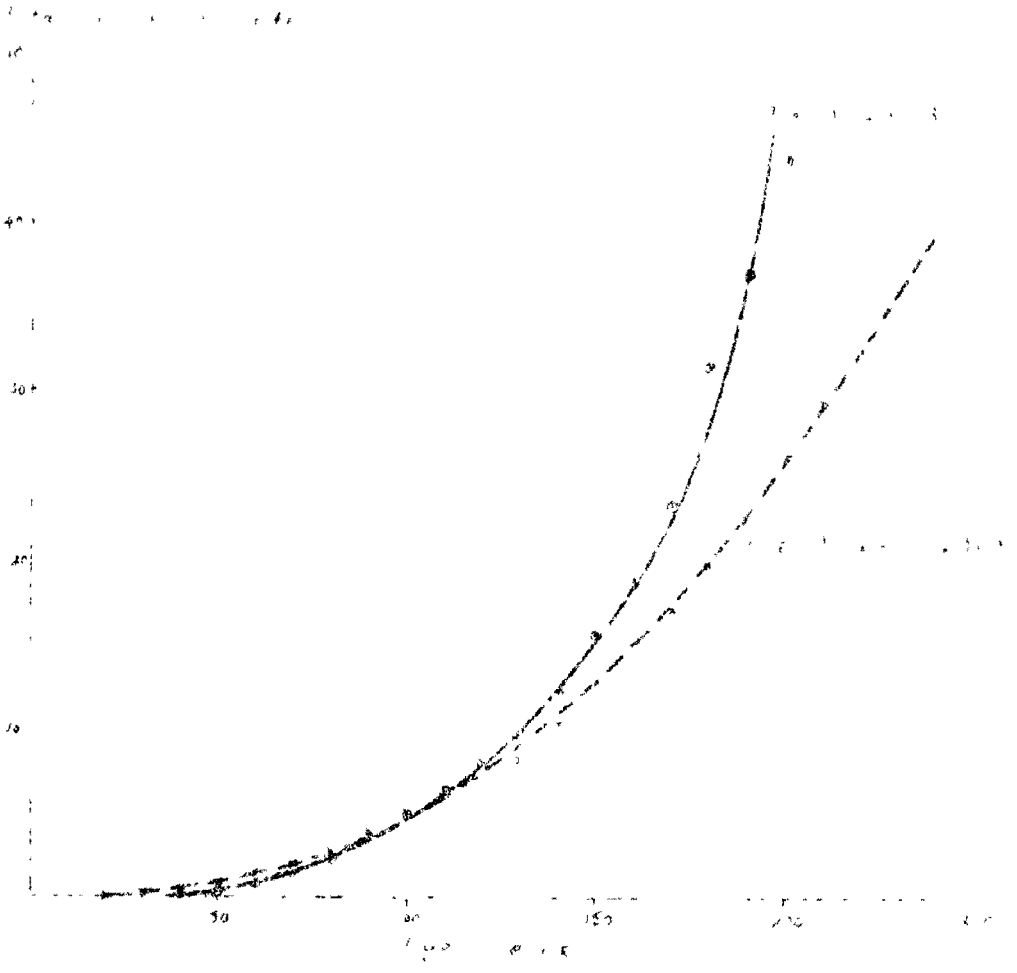

Fig. 34 - Main trunk volume plotted against tree age, Craigieburn Range (Association D 1). Each graph represents the mean values for ten trees.

The growth rates quoted for volume refer to the main stem only, between the ground level and the highest parts of the tree. A crude estimate of the volume growth of the main branches, i.e.

the first, second and larger third order branches, is approximately 25 per cent of that of the main trunk. This approximation has been arrived at by estimation of the diameters and lengths of these branches on the twenty sample trees and by reading off the appropriate volume from the volume table in Appendix 14. Each branch was dealt with as if it were a small tree.

The volume increment figures above would refer only to Association D 1 Nothofagus solandri trees. In some of the associations the growth would be much slower. For instance in Association A 1 the mean stand height is only 17.4 feet and trees seldom reach a diameter breast height of greater than 10 inches. In this association the fully grown tree would have a main stem volume of about 5 cubic feet (see App. 14). This spread over a life of about 200 years would give a mean annual increment of around 0.025 cubic feet per year.

4.3.5. Maximum tree age

P. Wardle (1963) records that 300 years is normally the maximum age for Nothofagus solandri, and the present study would certainly support this record. Occasionally, however, healthy trees with up to 360 distinct growth rings do occur.

4.3.6. Stand growth and structure

In the Nothofagus solandri associations C 6, D 1, and D 2 which form the bulk of the forest on the eastern side of the Main Divide in the South Island and in the central North Island, the basal area of the closed stand tends to be fairly constant. Measurement of basal area over bark on 49 tenth-acre plots taken from a range of sites in the Kaweka Range, the head of the Buller catchment, the Rakaia catch-

ment and the Waimakariri gave a mean of 24.91 $\pm$ 1.11 (P = 0.05) square feet per tenth acre. The extreme range, with the exception of one tenth acre plot which had in it an unusual concentration of large trees and exceeded 40 square feet basal area, was from slightly less than 20 to slightly more than 30 square feet. It is possible thus to assume a mean basal area of around 250 square feet per acre for stands in the above associations.

Even though the basal area remained fairly constant in the forty-nine plots, the number of stems varied considerably from one plot to another. For instance one tenth-acre plot in the Travers Valley which had a basal area of 26.63 square feet contained 526 stems while another in the Kaweka Range with a basal area of 26.58 square feet contained only 18 stems. To retain the basal area at such a constant level regardless of the number of stems must mean than when the basal area drops below about 250 square feet per acre, the vacuum formed is rapidly filled with ingrowth from advance growth seedlings. Conversely, if growth in the adult tree is still capable of replacing loss due to mortality and maintaining the basal area in the region of 250 square feet per acre, the advance growth is held in check.

From observations made during the present study and from supporting increment core counts in a number of stands in the above associations, it is apparent that most of the low complexity Nothofagus solandri forests are composed of mosaics of single aged, two aged or sometimes three aged stands and are seldom truly mixed aged (see Fig. 35). The size of these stands is variable but they are frequently quite large, and may be in the vicinity of tens of

Fig. 35 - Stand of Mountain beech, Clarence River, which shows how a 2 aged structure may develop. The canopy has opened up probably as a result of pin-hole borer attack. Following this opening up, the advance growth seedlings have been released.

acres. It is probable that at least the largest of these uniform areas results from catastrophe, as, especially at higher altitudes, the Nothofagus solandri forests are subject to extreme damage from snow-break (see Fig. 36), wind-throw and insect attack by pinhole borer, Proteodes carnifex and probably others. Fire, at least in Maori and European times has probably also been instrumental in producing such stands.

If 250 square feet per acre is accepted as the approximate basal area of the closed stand and if diameter growth can be calculated, then it is possible to calculate the average pattern of mort-

ality and basal area growth throughout the life of these stands. It is known from Fig. 31 that it takes seedlings about 25 years to reach breast height. A radial under-bark growth of about 28 rings per inch can be assumed for associations C 6, D 1 and probably also D 2 (see Table 12), Section 4.3.3. Thus average breast height diameter under-bark growth is 0.072 inches per year. To this must be added the contribution made to diameter growth by the bark.

Fig. 36 - Damage in mountain beech forest in the Craigieburn Range resulting from a snow storm during June 1968 (Photo by K. Platt).

Bark thickness was measured using a Swedish Bark Guage, on four sides of 48 stems of varying diameter, throughout associations C 6, D 1 and D 2, and the average bark thickness of each tree was calculated. The regression relating twice bark thickness and diameter at breast height over bark was calculated. The regression

is as follows:-

$$Y = 0.045 X + 0.116 \quad (r = 0.932, P < 0.001)$$

Where Y = 2 times bark thickness

and X = Diameter at breast height over bark.

Using this formula it is possible to calculate twice bark thickness, or bark diameter, for any diameter of tree and thus it is possible to calculate the bark growth which occurs with any increase in the diameter of the trunk at breast height. For instance an increase in the under-bark diameter at breast height of 0.072 inches is related to an increase in twice bark thickness of 0.0038 inches. As 0.072 inches represent the mean annual increment of diameter at breast height under bark, the mean annual increment of diameter at breast height over bark is 0.0758 inches or near enough to 0.08 inches.

If it takes 25 years for stems to reach breast height and subsequently the mean diameter breast height over bark increment is 0.08 inches per year, then trees in a 75 year old stand should have a mean diameter of 4 inches. To provide a basal area of 250 square feet per acre would require 2873 stems per acre. Assuming that each of these stems put on a further 0.8 inches of diameter in the next ten year period this would mean that the number of stems would have to be reduced to 1984 stems per acre to maintain 250 square feet acre basal area. Thus some 890 stems or 30 per cent of the original stems would have to die. The basal area increment on the trees which survived throughout the ten year period would be 77.4 square feet per acre. Thus the annual mortality in a 75 to 85 year old, even-aged stand would be 3 per cent and annual basal area

increment would be 7.74 square feet per acre. In a stand 175 years old there would be a reduction from 318 to 280 stems per acre in ten years and a compensating basal area increment on the surviving trees of 30.5 square feet per acre. In this case the annual mortality would be 1.2 per cent and the annual basal area increment would be 3.05 square feet per acre. In an older stand, 275 years of age, there would be a reduction of ten trees per acre in ten years, i.e. from 127 to 117 stems per acre, and a basal area increment of 19.8 square feet per acre. This would represent an annual mortality of 0.08 per cent and an annual basal area increment of 1.98 square feet per acre.

By means of calculations such as those above, the pattern of basal area increment and mortality throughout the life of an average, even-aged, low complexity stand of Nothofagus solandri has been derived and this is shown in the graphs in Fig. 37.

The above figures and graphs relate only to mortality resulting from competition within the stand. Whereas normally this is the major cause of mortality in the younger and middle aged stands, other causes relating to over-maturity and senescence would be expected to become increasingly important as the stand approaches 300 years of age. Thus it would be expected that mortality percentages would again increase in the older stands producing a basal area vacuum to be filled with ingrowth. Within a strongly competing stand the uniform age structure would tend to be carried at least for several generations after any disaster, and this is apparently what happens as few examples approaching normality are in fact to be seen. Regeneration released in temporary openings

is invariably suppressed before reaching the canopy and subsequently dies.

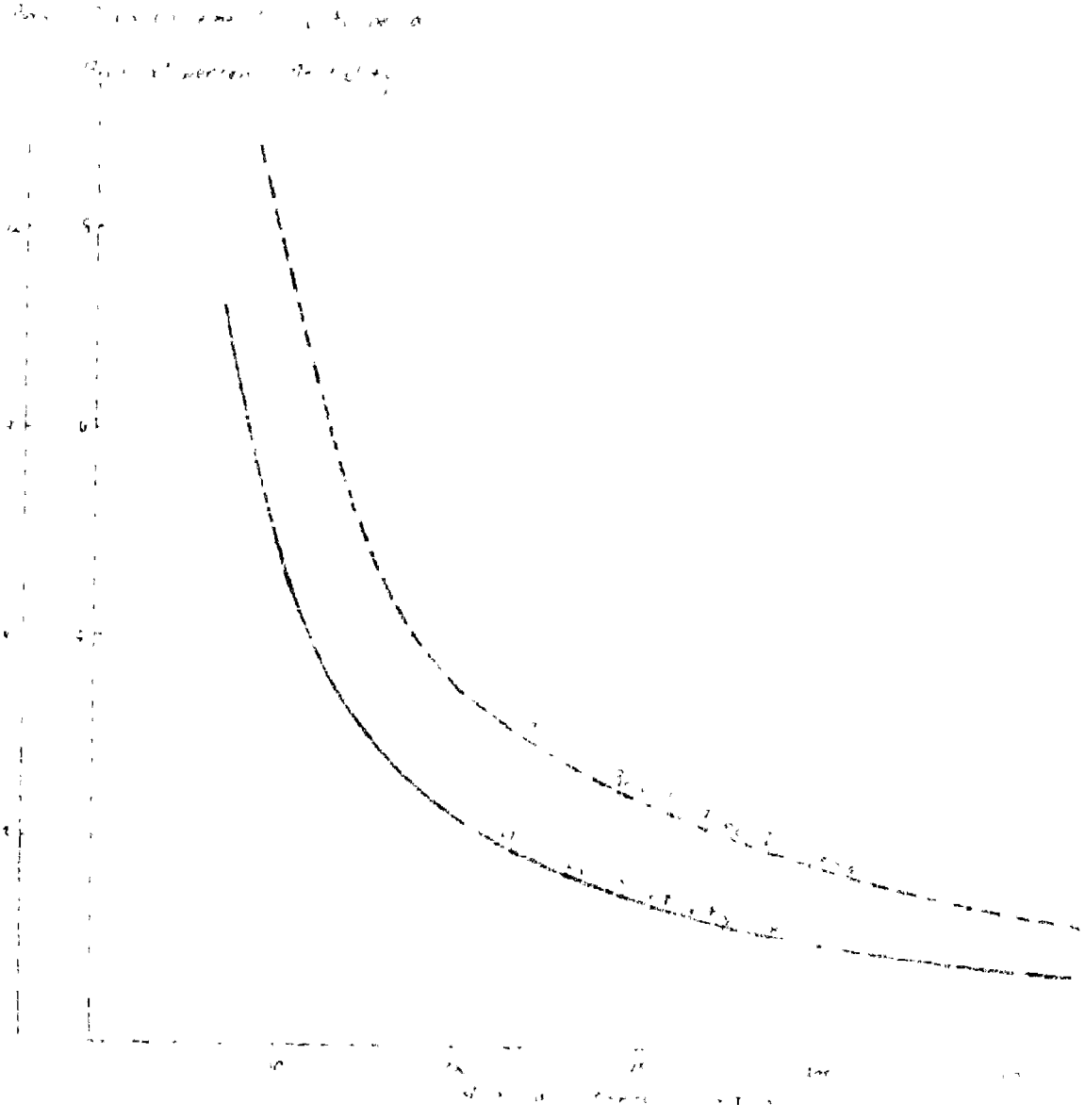

Fig. 37 - Annual basal area increment and annual mortality resulting from competition in even-aged stands of Nothofagus solandri. (Hypothetical example based on a maximum standing basal area of 250 square feet per acre in competing stands, and a mean diameter increment for all diameter classes of 0.08 inches at breast height over bark per year.)

The above graphs and figures on mortality and basal area increment are largely hypothetical but to test their reality would require

periodic measurement throughout the life of a large even-aged stand, and apart from a study carried out by Elder (pers. comm.) on a single tenth acre plot in the Kaweka Range at 3100 feet altitude in forest established after a fire at around the year 1870, no such information is available. Elder's stand gave a mortality rate of 2.3 per cent per year between when the stand was 70 and 87 years of age, a figure not too far removed from the hypothetical 3 per cent calculated from this study. Further in this 17 year period the stand showed constant basal area. However, in the following ten years the mortality rate of Elder's stand was only 0.6 per cent, a figure much lower than that suggested above and the plot showed a slowly rising basal area.

To study the structure, mortality and basal area growth of the 'normal', balanced-aged stand of Nothofagus solandri the diameter class frequencies of the same 49 tenth acre plots were pooled. In each plot the diameters at breast height over bark of all stems over 0.5 inch had been measured to the nearest tenth inch and sufficient increments taken to establish that diameter growth rates were comparable with the means for associations C 6 and D 1, shown in Table 12, Section 4.3.3. Two inch diameter classes, from 0.5 inch diameter breast height over bark, upwards, were used. Frequencies for each class were calculated and then converted to a per acre basis and the histogram of diameter frequency shown in Fig. 38 was derived. According to Meyer, Recknagel, Stevenson and Bartoo (1961), the relationship between frequencies of stems in successive diameter classes should be in the form of an inversed-J-shaped curve of the type

log Y = a + b X where Y represents the frequency and X the diameter class. If the 0.5 to 2.5 inch diameter class is ignored, this relationship is strongly apparent in Fig. 38, and in fact the relationship for Nothofagus solandri can be represented by the following regression equation:-

log Y = 2.995 - (0.123) X (t = 0.005)

where Y = the frequency of stems in a two inch diameter class

and X = the mid point of that class.

The anomalous 0.5 to 2.5 inch diameter class has only 192 stems per acre whereas the regression relationship suggests that it should in fact have 646. The difference between actual and predicted values in this class would have been put down to inadequate sampling had there been great variation between these two values in the remaining 16 diameter classes, but in fact the relationship in these was a strong one so it is necessary to accept the depression in the 0.5 to 2.5 inch diameter class as real and offer suggestions as to the cause. The 0.5 to 2.5 inch diameter class represents the saplings of the stand up to the age of about 55 to 60 years ago and this coincides approximately with the period over which terrestrial browsing mammals have become established in these forests. It is known that they feed on the seedlings and saplings of Nothofagus solandri and it would not be an unreasonable assumption that the depression is related to their presence.

If the mean basal area of the component 49 stands measured in this study is accepted, then the basal area of the balanced mixed-aged stand becomes 249.1 square feet per acre. If on the other hand the regression model is accepted, the basal area becomes 238.2 square

feet per acre and number of stems per acre greater than 0.5 inch diameter breast height over bark becomes 1493.6. Of these there

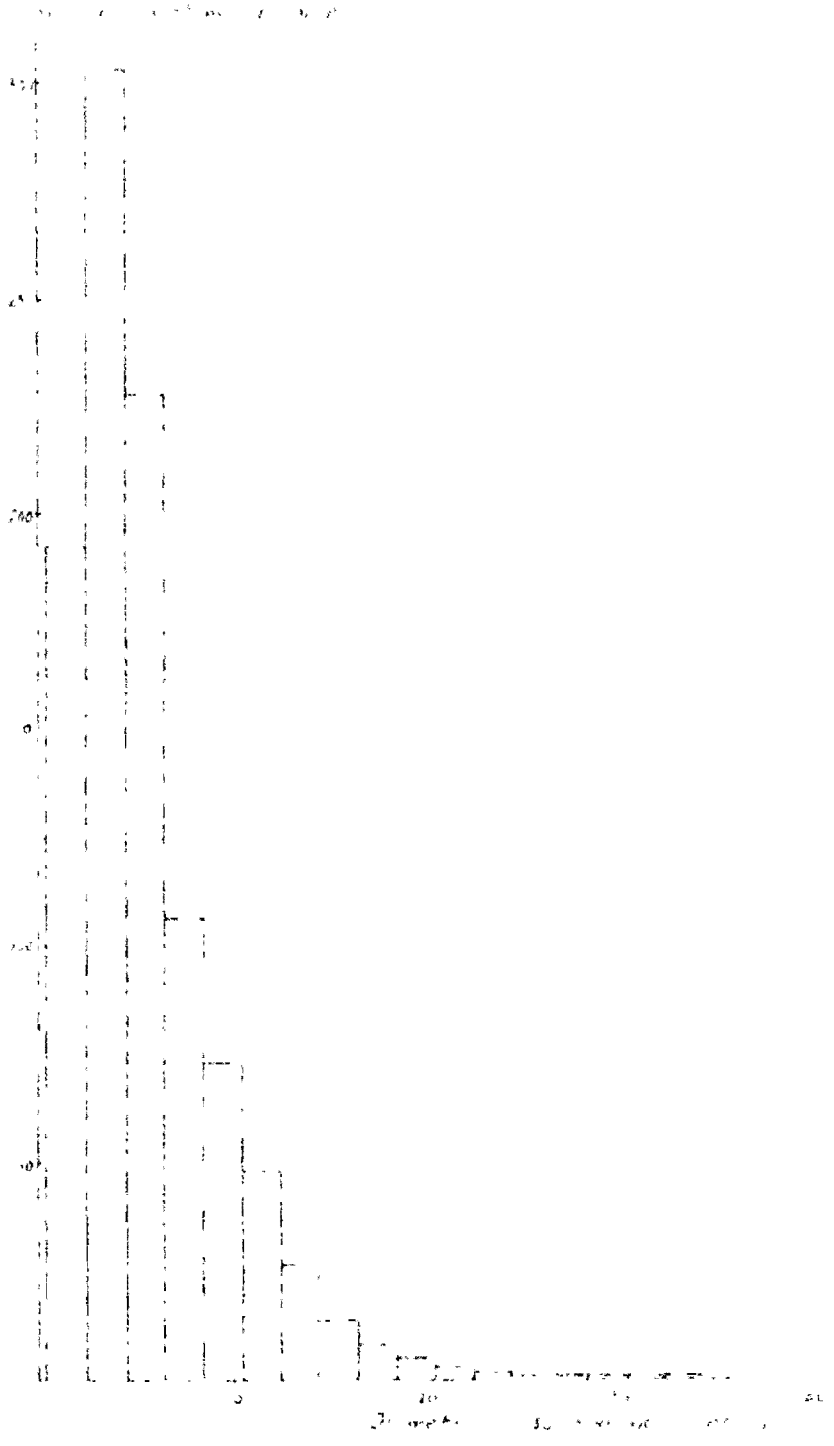

Fig. 38 - Diameter (breast height outside bark) frequencies in balanced mixed aged stands of Nothofagus solandri. Derived by averaging diameter class frequencies from 49 tenth acre plots selected from associations C 6 and D 1 in the Kaweka Range and in the Buller, Waimakariri and Rakaia River Headwaters.

is a mortality of 646 stems over the period it takes for the mean tree in each diameter class to progress into the mean position in the next highest diameter class. Accepting a mean growth rate of 0.08 inch diameter at breast height over bark, per year, this would take 25 years. So the annual mortality is 26 stems or 1.73 per cent of the stand. Of course this mortality rate would not be spread regularly over all the diameter classes but would be much higher in the smaller diameter classes than in the larger ones. In fact it would be in the proportion of the number of stems present in each class as given by the regression equation. Ingrowth from seedlings and saplings less than 0.5 inch diameter breast height over bark would be in the vicinity of 646 stems over 25 years, i.e. 26 stems per acre per year, to maintain a balanced mixed-aged stand structure.

Basal area increment over the 25 years required for each diameter class to move into the next highest class is in the region of 102.6 square feet per acre. This figure is calculated assuming maintenance of the same balanced mixed-age structure and consequently must be balanced against basal area mortality. The annual basal area increment is therefore 4.105 square feet per acre per year. The bulk of this increment is put on the poles which have diameters at breast height over bark lying between 2.5 and 8.5 inches, and in fact 60 per cent of the basal area increment occurs in this region.

It was possible to combine the results from the 49 tenth acre plots taken from both North Island and South Island dry Nothofagus solandri forests for the consideration of mortality, diameter structure, ingrowth and basal area growth of the stand, in that close-

to-constant diameter growth rates were being dealt with both from plot to plot and throughout the life of the tree. However any consideration of standing volume and volume growth must bring in the element of height growth and mature stand height and these vary considerably from one area to another. If, however, the diameter class frequency of Nothofagus solandri as calculated from the above 49 plots is accepted, and the mean diameter growth under bark for Nothofagus solandri of 0.072 inches is also accepted and if the height growth rates calculated from the stem analysis at 3000 feet and at 4400 feet in the Craigieburn Range separately are superimposed on this, it should be possible to use this information to calculate the range of standing volume and volume increment which might be expected from association D 1 stands. One problem does remain, however, in that the diameter class frequency of the normal stand has been calculated for over-bark measurements while the two way tree volume table (see App. 14) from which standing volume is read has had to be calculated for under-bark measurements since it was derived from stem analysis.

By using the regression for bark thickness on diameter at breast height over bark it is possible to calculate bark diameter for the mid-points of each of the stem diameter classes in the balanced mixed-aged stand and by subtracting this figure from the over-bark diameters the diameter at breast height under bark for each class may be calculated. By assuming a diameter breast height under bark growth of 0.072 inches per year and by allowing 25 years for a seedling to reach breast height, we can now calculate the mean age of the mean tree in each diameter class. The total height

of these mean trees is read off from the graphs in Fig. 31. By referring to the two-way volume table (App. 14), it is now possible with this height and diameter breast height under bark information to arrive at the total stem volume under bark of the mean tree in each diameter class. The inversed-J-shaped curve regression on diameter frequency distribution may be used to determine how many stems occur in each diameter class of a balanced, mixed-aged stand so the total stem volume for each diameter class can now be calculated, and by adding these, the total wood volume of the mixed aged stand. The total main stem wood volume, if the mean tree heights at 3000 feet altitude are accepted, is 5800 cubic feet per acre. If on the other hand the 4400 feet altitude mean heights are accepted, the volume per acre becomes 3900 cubic feet. The breast height over bark diameter class which contained the peak standing volume at each level was the 8.5 to 10.5 inch class (see Fig. 39).

If a diameter breast height under bark growth rate of 0.072 inches per year is accepted, and if the bark growth is calculated by comparing the bark thickness of the mean tree of each 2 inch diameter class in the normal stand then it can be simply calculated that it takes 26 years for the mean tree in each 2 inch diameter class to move to the mean position in the next highest class. To maintain a normal structure the number of stems in each diameter class must remain constant and, by assuming that it does, it is possible to calculate the volume increment on the stems which survive the shift from one diameter class to the next. If the volume increment for all diameter classes is summed for one such shift and

to this is added volume increment from ingrowth, then it is possible to calculate the annual volume increment per acre by dividing the total by 26 (the number of years required for the shift to occur). The volume increment, and in balance, the volume mortality is 95 cubic feet per acre for 3000 feet altitude, and 65 cubic feet per acre for 4400 feet altitude. If 25 per cent for main branch volume is added, the total wood increment becomes 119 and 81 cubic feet respectively.

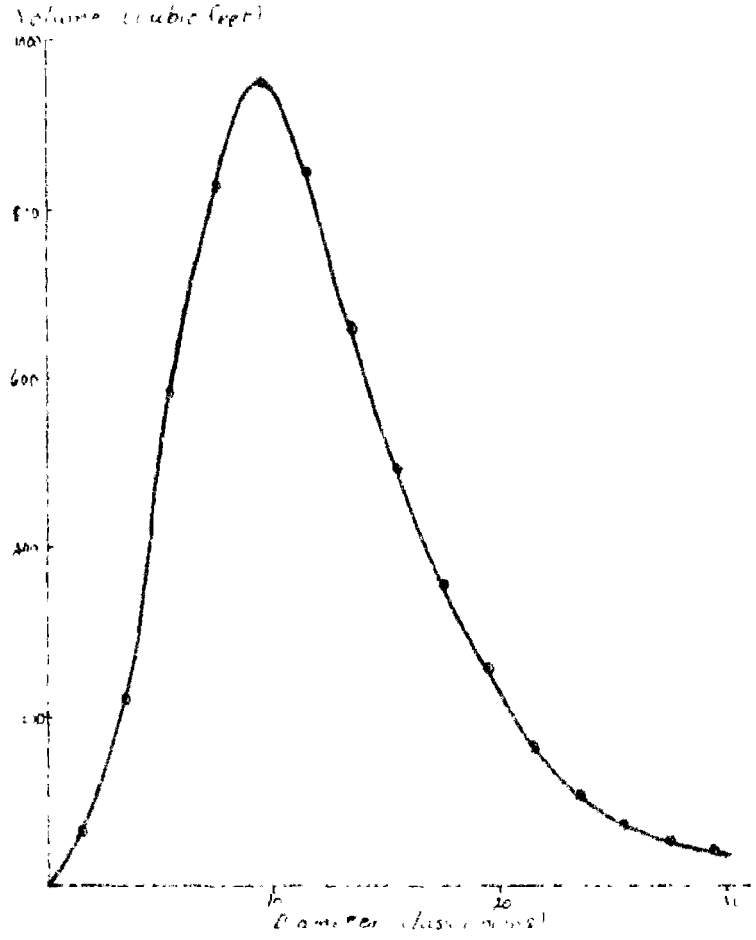

Fig. 39 - Main stem volume distribution for over-bark diameter at breast height classes in a normal stand. Tree height for each diameter class is as for 3000 feet in the Craigieburn Range. (See Fig. 31).

Specific gravity measurements were carried out on samples of wood taken from trees at 3400 feet in the Craigieburn Range and it was established from these that the oven dry weight of this wood was 30.54 $\pm$ 2.05 (P = 0.05) lbs per cubic foot. Thus dry-weight wood production is 3634 lbs per acre in the normal stand at 3000 feet altitude and is 2474 lbs per acre at 4400 feet. The annual dry-weight leaf and twig production from the crown of the stand has been calculated from the collections in the seed trays at a number of sites in the Kaweka and Craigieburn Ranges and at Mt Thomas (see App. 10). The production from eight trays over a period of three years gave a mean figure of 3320 lbs per acre per year at 3400 feet and 2734 lbs per acre per year at 4400 feet altitude in the Craigieburn Range. The total above-ground dry matter production of the Association D 1 mountain beech stands at 3000-3400 feet altitude must be about 3320 + 3634 lbs per acre per year, i.e. 6954 lbs, while at 4400 feet it would be about 2474 + 2734 or 5208 lbs per acre per year. These figures are approximate only. Annual bark production is ignored, and main branch volume is an estimation only ~~and no allowance~~ has ~~been~~ made for root growth.

This sub-section on stand growth and structure applies only to the dry forests in the central region of the North Island and east of the Main Divide in the South Island. The associations which make up the bulk of these forests, C 6, D 1 and D 2, have fairly regular diameter growth rates ranging from around 25 to 30 rings per inch, and the basal area of the closed stand is fairly constant at around 250 square feet per acre. This growth rate and this basal area does not apply to all associations. Association A 1 which is normally

restricted to areas of slow weathering parent rock on the west side of the Main Divide, has a diameter growth rate less than one quarter of that given above and the standing basal area is also much smaller. The mean height for the association is only 17 feet and in some stands it is less than breast height. Associations B 2 and B 3 which occur on the western side of the Main Divide, in areas of poor drainage, each have about 60 rings to the inch at breast height (see Table 12). The mean standing basal area from 17 tenth acre plots measured in these associations was 193.59 $\pm$ 23.11 (P = 0.05) square feet. Only 105.29 $\pm$ 21.41 (P = 0.05) square feet of this was made up of Nothofagus solandri. The rest was of Dacrydium biforme, mountain cedar and other tree and shrub species. The basal area and volume growth in these stands is difficult to estimate as the growth rates of the species other than Nothofagus solandri are not sufficiently well known. However, it is certain that it is considerably less than that quoted above for the drier, more monotypic forests.

4.3.7. Summary and Conclusions

Bud opening in Nothofagus solandri occurs sometime between late September and early December. The buds go through a period of elongation which may proceed over two months before bud-burst actually takes place. During this period cold temperatures may actually halt elongation temporarily but permanent damage to the buds does not necessarily result.

The date of bud burst is delayed with increase in altitude by almost two weeks per thousand feet. It is also later in the prox-

imity of frost pockets and possibly in areas of frequent fog, and may vary from season to season by as much as one month. The period over which most of the growth occurs is also much reduced with increase in altitude. Near the bushline in the Craigieburn Range, 80 per cent of the total annual height growth occurs within 1½ months, while at Rangiora near sea level the same proportion of the annual growth takes 4½ months to occur. Some growth continues at all altitudes up until about the end of March.

Shoot extension occurs in a number of bursts. The first burst is an expansion of leaves already present in the over-wintering bud. After this a new bud tends to be formed. Near the bushline there may only be one burst of growth on the terminal and lateral shoots in a season, but at lower altitudes there may be up to three bursts of growth on terminal shoots and two on lateral shoots.

The leaves of Nothofagus solandri are generally shed during the growing season following the one in which they are produced. The peak fall occurs from December through until the end of April but again there is a delay of two to three weeks per thousand foot increase in altitude. Twig fall tends to be deciduous, though not to the same marked degree as leaf fall. Otherwise the pattern is much the same as for leaf fall.

Height growth of Nothofagus solandri in sheltered, low altitude sites can be as much as 36 inches per year. In the open the growth on the terminal shoots decreases markedly with increase in altitude but there is little change in the growth of the lateral shoots. This change in the ratio of terminal to lateral growth results in a change in growth form from a tall tree at lower altitudes to a short

squat, often semi-prostrate tree near the bushline. A reduction in the terminal growth rate also tends to occur when Nothofagus solandri is planted in localities such as Rangiora which are too dry to support it naturally. Though open grown saplings show a reduction in height increment with an increase in altitude, there is little change within the stand. The mean annual increment of saplings within competing stands in the Craigieburn Range was 3 inches both at 3000 feet and at 4400 feet altitude.

The pattern of height growth throughout the life of the tree follows the normal sigmoid pattern. The tree reaches about half its total height after 80 to 90 years and by 150 years of age it approaches its maximum height. From then or until the tree dies much of its growth effort is involved in crown extension. The ultimate height attained by trees of Nothofagus solandri depends on the type of site and can thus be related to the associations, (see Sect. 3) in which it occurs. The ultimate mature height may vary from 1 foot 6 inches to over 80 feet.

The rate of diameter growth at breast height is fairly regular throughout the life of the tree. It is also much the same at different altitudes within one Nothofagus solandri association but varies considerably between one association and another. Some associations have only twenty to thirty rings per inch of radius while others may have over 100 rings per inch. The slowest growth rate measured was 179 rings per inch while the fastest was 8.5 rings per inch.

As a result of the regular diameter increment throughout most of the life of the tree, the basal area and volume increments increase

at progressively greater rates with increase in age. In association D 1 the annual increment is less than 0.02 cubic feet per year during the first 50 years. However from 150 to 200 years of age it can be as high as half a cubic foot per year. Growth in volume can vary considerably from one association to another. For instance in Association A 1 the mean annual increment throughout the life of the tree is less than 0.03 cubic feet per year.

The maximum age of Nothofagus solandri is generally around 300 years but occasionally trees may reach 360 years of age.

In Associations C 6, D 1 and D 2, which are of low species complexity and which form a large proportion of the forest on the east side of the Main Divide in the South Island, and in the central North Island, stand basal area is held fairly constantly around 250 square feet per acre. Forest in these associations is usually composed of mosaics of even-aged stands, each probably resulting from catastrophe some time in the past. These even-aged stands have around 2900 stems per acre at age 75 but competition reduces this to 318 stems per acre at 175 years, and at 275 years of age only 127 stems remain. The annual basal area increment at these ages is respectively 7.74, 3.05 and 1.98 square feet per acre.

The diameter structure of the balanced mixed-aged stand has been calculated from the measurements on 49 tenth acre plots. It can be expressed by the regression $\log Y = 2.995 - (0.123) X$ where Y equals the frequency of stems in a two inch diameter class which has a mid-point X. The mean number of stems greater than 0.5 inches diameter breast height in such a stand would be 1494 and the mean annual mortality would be 1.73 per cent or 26 stems per acre per year.

Hence ingrowth from less than 0.5 inches diameter breast height would also have to be 26 stems per acre per year if a balanced stand structure was to be maintained. The annual basal area increment is a little over 4 square feet per acre per year and the bulk of this is put onto stems with diameters at breast height ranging from 2.5 to 8.5 inches.

Standing volume and volume increment was calculated assuming the above balanced diameter structure and superimposing on this the age-height relationship of two stands, one at 3000 feet altitude, and one at 4400 feet altitude, in the Craigieburn Range. The total main stem wood volume calculated for 3000 feet altitude was 5800 cubic feet per acre, while that for 4400 feet was 3900 cubic feet per acre. Total wood increment for the main stems and main branches was respectively 119 and 81 cubic feet per acre per year. The dry weight of this annual wood production came to 3634 lbs per acre at 3000 feet and 2474 lbs per acre at 4400 feet. The annual dry weight leaf and twig production measured from the seed trays (Section 4.1.2.) was 3320 and 2734 lbs per acre per year for approximately the same altitudes, and thus total above ground dry matter production for stands in associations C 6, D 1 and D 2 can be expected to be in the vicinity of 6954 lbs per acre per year at 3000 feet and 5208 lbs per acre per year at 4400 feet.

Stands measured in associations B 2 and B 3 which grow in areas of poor soil drainage had a mean basal area of only 193 square feet per acre and only a little over half of this was of Nothofagus solandri. In these associations diameter growth rates are much

slower and consequently basal area growth, volume growth and dry matter production must be considerably below those given above. Volume and basal area growth probably reach their minimum in Association A 1.

SECTION 5 DISCUSSION

It has been stated in the introduction that the purpose of this thesis was to investigate the life history and ecological behaviour of Nothofagus solandri, and to relate variation in behaviour to habitat and thus attempt to explain the present geographic and ecological distribution of the species. With this aim in mind the distribution of the species, both ecologically and geographically, was described in Section 2 and it was pointed out in the summary and conclusions that although initially there would appear to be many contradictions in the distributional pattern of the species, most of these would be explained by an hypothesis that Nothofagus solandri is a species with a wider range of tolerance than most New Zealand tree species, for harsh conditions for growth such as occur where rainfall is low, at high altitudes and under conditions of poor soil development and poor soil drainage, but that it is also a species which has a low ability to compete with other trees and shrubs where conditions are improved and the site becomes more ideal for forest growth. In Section 3 the wide range of habitat which the species occupies is sub-divided, not initially with reference to measurement of the physical factors of the environment, but with reference to the composition of the plant communities. In this section 23 plant associations were defined and the habitat of each was broadly described. In Section 4 the life history and variation in the life history of Nothofagus solandri is described, and it is demonstrated how much of this varia-

tion can be related to habitat.

Many aspects of the methods used and of the results obtained in this thesis have been discussed in the appropriate section in the text. The main purpose of this discussion is merely to weld together the findings of the above three sections in an attempt to explain which facets of the life history of Nothofagus solandri permit it to occur within associations which occupy such varying habitats, and which facets are limiting to its distribution. Finally in this section, ways in which this study can be of aid in formulating a basis for the management of Nothofagus solandri forests will be briefly indicated.

The associations which occupy the driest sites are C 1, C 4, D 1, F 1, F 3 and G 1 (see Table 2). Of these, Associations D 1 and G 1 probably include the driest Nothofagus solandri forests in the country. Both have few associate shrub and other tree species and in both, if a stand is destroyed by fire or other means, the first plants to occupy the cleared area are usually herbs or grasses. The return to a forest cover is usually by slow marginal migration of the bush edge during which seedlings seldom become established further than about parent tree height away from the seed source (see Fig. 20A, Sect. 4.2.3.), though occasionally a small shrub or a large tussock of grass may serve as a nurse to a seedling further out. Associations C 1, C 4, F 1 and F 3 do not occupy quite such dry sites and in each of them there are a number of associated small tree and shrub species. When a stand in one of these associations is destroyed, a tall scrub cover which is often dominated by Leptospermum species usually develops (see Cockayne, 1926 pp 61-62).

Once the scrub cover approaches maturity it acts as a nurse crop for seedlings of Nothofagus solandri. In this situation seedlings of the species may be regularly found as far as ten times tree height away from the parent (see Fig. 208), and the return to forest is relatively rapid. If seedlings can be found this distance away from the parent tree where there is a development of scrub following clearing, then obviously the distance of seed dispersal is not the cause of the slow marginal return to forest as is the case in Associations D 1 and G 1. The cause must be related to some other stage or stages of forest establishment, ones which would be aided by the provision of a shade similar to that of a mature Leptospermum scrubland. Trials carried out on germination and early seedling development (see Sect. 4.2.4.), at Rangiora, probably provide part of the answer. In these trials only 4 per cent of sound seed sown in the open germinated and the seedlings which did germinate all died in the first summer. Where light shade was provided, though, 54 per cent of the seed germinated and 78 per cent of the seedlings survived the first summer. It takes approximately two months after sowing seed of Nothofagus solandri for the first foliage leaves to appear and during this time the germination media must remain moist. It appears that a raw litter cover such as is found near the margin of a parent stand, or under a mature Leptospermum scrubland provides the right conditions but that a grassland apparently does not because the dense surface feeding roots of the grass and the lack of restriction to air movement prevent humid conditions from being maintained in the germination media.

Even if isolated seedlings do germinate and manage to survive

the first summer in the open grassland, their chance of ultimate survival is still fairly slim. The older seedlings are still very susceptible to drying conditions and even saplings often show die-back of the terminal shoots. The reason for this die back is not fully understood, but it does seem to be related to periods of strong dry wind rather than to soil moisture becoming limiting.

In summary it appears that the low rainfall limits of distribution of Nothofagus solandri are almost certainly primarily determined by the moisture requirements for germination and first year seedling survival, and also, though to a lesser extent, by the apparent inability of the older seedlings and even saplings to withstand indefinitely full exposure to dry winds. Whereas Nothofagus solandri seems to have little difficulty in maintaining itself on marginal rainfall sites once it has established an initial canopy, it does have difficulty where there is no canopy, either of its own, or of scrub species.

Although the dry associations include some of the most extensive stands of Nothofagus solandri in the country, they do not represent ideal growing conditions for the species. For instance the mean stand heights for Associations D 1 and G 1 are only 44 and 31 feet. In other associations the mean stand may exceed 60 feet. Diameter growth likewise tends to be below maximum in these associations, though not excessively so. For instance, in Association D 1 there is a mean of 29.4 annual growth rings per inch of radius compared with a mean of 23.3 for Associations C 5.

The Nothofagus solandri associations which occupy the poorest drained sites include A 1, B 2, B 3, B 4, and C 2. Of these,

Association B 2 probably includes most of the stands of Nothofagus solandri which occur where the drainage is marginal for the species. In this association the diameter growth rate of Nothofagus solandri, and the mean stand height, is well below that for most of the other associations. There are in the vicinity of 60 growth rings per inch of radius and the mean height is a mere 37 feet. The contribution to the community of other tree and shrub species is quite high and in fact Nothofagus solandri makes up only a little over half of the stand basal area and other tree species such as Dacrydium biforme are equally important. There are probably two main reasons why Nothofagus solandri can exist in a complex community of this nature. The first is that the growth rates of the other major tree and large shrub species such as Dacrydium biforme, Phyllocladus alpinus and mountain cedar are probably equally slow or even slower than Nothofagus solandri. (P. Wardle 1963, gives the growth of Dacrydium biforme as 25-50 growth rings per cm of radius and mountain cedar as 14-40 per cm). The second reason is that there is a low basal area. In Section 4.3.6. it has been shown that in the monotypic associations such as D 1, the mean basal area of the mature stand is around 250 square feet per acre, and there is evidence that once the basal area drops far below this value, 'advance growth' becomes released. In Associations B 2 and B 3, the mean basal area of the 17 stands sampled was only 194 square feet per acre. These associations are thus in a fairly open condition and light is therefore probably not a strongly limiting factor for seedling growth under these stands. Certainly the carpets of suppressed advance growth seedlings so typical of the monotypic associations are not generally a feature of the Association

B 2 stands. The availability of sites suitable for seedling establishment is probably the factor which retains these stands in an open state and must ultimately be the factor which determines the distribution of Nothofagus solandri on poorly drained land. It has been noted that small seedlings of Nothofagus solandri can be found throughout these stands on the thick moss layers which cover much of the forest floor, but older seedlings are restricted to raised ground around the bases of the larger trees and on the stumps of dead trees, and on logs. Obviously the pre-germination, germination and early seedling phases of the life history are not the factors which limit the distribution of the species in these poorly drained sites. Apparently it is the survival of older seedlings which is important since they must have at least some of their feeding roots above the level where the soil is subjected to repeated waterlogging.

The Nothofagus solandri association which occupies sites where the soil development is thinnest is Association A 1. This association includes the shortest and the slowest growing stands of the species recorded. Here mature stands only 1 foot 6 inches high occur and some growth rates of over 170 rings to the inch have been measured. The mean stand height is only 17.4 feet and the mean growth rate is 118 rings per inch of radius. The position which Nothofagus solandri occupies in this association, which is again a complex one, is much the same as in Association B 1. Here again the slow growth rates of the associate tree and shrub species, and the open nature of the community are the reasons why Nothofagus solandri is present. Frequently there are quite large gaps in stands of this association with no trees or shrubs at all. Here again it

is the low availability of sites suitable for seedling establishment which retain these stands in an open condition, though the limitation in this case is not usually waterlogged soil but rather a complete lack of soil and what soil there is, is frequently limited to cracks and crevices in otherwise solid, slow weathering bedrock.

In Section 4, a number of experiments are described which were designed to study the changes which occur in the regeneration and growth of Nothofagus solandri as the upper altitudinal limits of the species are approached. The results from these experiments which were mostly carried out in the Craigieburn Range, show that with gain in altitude there is a considerable reduction in the quantity of seed which is produced and that the quality of this seed becomes much poorer. This deterioration in seed quality is possibly related to the much shorter time that the seed has in which to ripen. Also germination percentages become much lower, first year seedling mortality higher and the growth of the seedlings, both in the first season and subsequently becomes considerably reduced at the higher altitudes. The terminal height growth in open-grown saplings near the upper limits of the species is only one quarter of what it is 1200 feet lower down the slope and the period over which this growth occurs is compressed into a much shorter period. Growth on the lateral shoots on the other hand, and growth on saplings in the protection of the parent canopy are not greatly affected. The maximum height the stand achieves is usually much less at the higher levels. Diameter growth shows little change with increase in altitude and nor does the standing basal area or basal area increment of the stand.

It is apparent that many facets of the life history of Nothofagus

solandri change with increase in altitude and probably the relative importance of these in determining the altitudinal distribution of the species varies from one area to another. For instance in the mid-Ruahine Range, the bushline which is of mountain beech has apparently disintegrated recently and the upper forest now consists of groups of old open-canopied trees with little regeneration over a dense Chionochloa tussock understorey. What apparently has happened is that the old stand has opened up suddenly, perhaps as a result of heavy snow, and there have been insufficient seedlings on the forest floor to fill the resulting gaps. Such sparsity of seedlings is quite a common feature in the upper forest where mountain beech forms the bushline and appears to result from the reduced seeding and germination of the species at these upper levels. As a result thick Chionochloa has been able to become established and consequently has reduced sites available to mountain beech regeneration. Here seed shed may well have been the instrumental factor in the determination of the altitudinal limits of the species. In associations such as C 6, D 1, D 2, D 3 and D 4 Nothofagus solandri usually forms a high but abrupt and regular bushline before giving way to a low scrub or tussock grassland. P. Wardle (1965) suggests that the abruptness of these bushlines depends on the relative susceptibility to damage by late frost of seedlings growing in the open, as compared with those under shade. Certainly the results of the present study would not contradict his suggestion. For instance, it would be unlikely if seed source was the primary cause of such a regular and abrupt bushline. The potential for germination is probably considerably less near the bushline than at lower levels

since there is a much shorter period over which soil temperatures are sufficiently high for it to occur. However, since climatic conditions at bushline must vary from year to year, the bushline would again be a staggered and irregular one if germination alone was the limiting factor and conditions for it were not modified by the presence of a parent canopy. Certainly studies on sapling height growth from within and outside of the stand suggest that the parent canopy exerts an increasing influence on the growth of Nothofagus solandri regeneration as the bushline is approached. As stated earlier, terminal growth measured on open grown saplings at bushline was only a quarter of that on saplings 1200 feet down the slope. On the other hand there was little difference in terminal growth between the two altitudes on saplings under the parent canopy.

Seedlings growing in the shade do not always perform better than seedlings grown in the open near the upper altitudinal limits of the species. It has been stated in the summary and conclusions to Section 2 that the upper limits of Nothofagus solandri descend rapidly as the coast, especially the West Coast, is approached, and the bushline which it usually forms towards the central regions of both islands gradually becomes taken over by other species. Usually Nothofagus solandri gives way to a bushline of silver beech which in turn may give way to kamahi, rata, mountain cedar and halls totara, or occasionally Nothofagus solandri itself may give way directly to these species. Nothofagus solandri tends to become restricted to plant communities on the harsher sites of poor drainage and poor soil development, such as those described earlier in the discussion, and its upper altitudinal limits and in fact its total distributional

pattern must be limited by an inability to compete efficiently with other tree and shrub species under conditions existing. Here, in contrast with the central regions where it forms the bushline it is probably the performance of the seedling under the canopy which must be limiting.

The rainfall, where Nothofagus solandri becomes restricted in its occurrence in this way, is generally much higher than where it forms a major component of the forest, and the physical conditions for forest growth, and for that matter for the growth of Nothofagus solandri, must generally be improved. That this is in fact so is suggested by the mean height of the Nothofagus solandri associations and by the diameter growth rate of the species. The associations which occur towards the high altitude, low rainfall, poor soil drainage and shallow soil development limits of the species are the shortest in height. The associations such as C 2, C 4, C 5, F 1 and F 2 which occur furthest away from these extremes tend to be the tallest. Of the associations sampled, the best diameter growth was from Association C 2. It is less in each of Associations A 1, B 2 and D 1 which, respectively, represent associations on poorly developed soils, poorly drained soils and towards the low rainfall limits of the species.

The limits of distribution of Nothofagus solandri under improved physical conditions probably relates to an inefficiency of the seedling to compete with other forest species under low light intensities. That Nothofagus solandri seedlings can persist for long periods under the shade of a dense parent canopy is fairly apparent from a study of the advance growth in the purer of the

Nothofagus solandri associations. This advance growth which serves as a seedling reservoir between successive seed years can survive up to 20 years without making much effective growth. It seems that it requires a reduction in the basal area of the stand to less than 250 square feet per acre before it becomes released. Species which can show effective growth in stands with basal areas of 250 square feet per acre or more must be favoured over Nothofagus solandri in forest composition. Unfortunately there has been little work done in New Zealand on the relative shade tolerance of the tree species, or on the total stand basal areas which they may achieve. Silver beech, which is a species to which Nothofagus solandri often gives way as conditions for forest growth improves, seems to form denser stands than Nothofagus solandri. Wardle, P. (1967) states that silver beech is reputed to be a more persistent species under heavy shade than the other species of Nothofagus and also its life span which Wardle (loc. cit) gives as around 600 years, is greater than that for Nothofagus solandri. All three factors would tend eventually to favour silver beech at the expense of Nothofagus solandri on a site where the physical factors of the environment favoured both species.

So far the factors which limit the distribution of Nothofagus solandri have been discussed. It remains to consider some of the properties of the species which permit it to occupy such a diverse range of habitats. The extent of the upper altitudinal limits are probably aided by its pattern of shoot extension described in Section 4.3.1. Near the bushline, eighty per cent of the total annual shoot growth of the species can occur in a period as short as 1½ months. Also if unseasonally cold conditions occur, bud burst can become

temporarily halted but may proceed again with apparently no ill effects once the temperatures again rise. Undoubtedly one of the factors which permits Nothofagus solandri to occupy poorly drained sites, and sites where there is a very poor soil development is the ability of the seedlings to grow very slowly and to concentrate most of the growth into the developing root system. The extreme variation which exists in the growth rate and growth form of the species has been referred to earlier. It is not fully understood just how much of this variation is related to genotypic differences between the different populations of the species. Certainly two varieties of Nothofagus solandri are at present recognised and apparently stable populations intermediate between these two varieties occur (see Sect. 2.3.). However experimental investigations into genotypic variation has been considered to be beyond the scope of the present study and will be discussed no further.

Management considerations will be only briefly discussed here. Many, if not all, of the results described throughout the text bear some relationship to the management of the Nothofagus solandri forests. The relative importance of these results depends on the primary purpose in the management of particular stands. If for instance it is ever decided to utilise Nothofagus solandri for production of pulp, then knowledge of the volume of wood produced as described in Sections 4.3.4. and 4.3.6., and of the light requirements for regeneration to occur (see Sect. 4.2.5.), become essential. If, perhaps, it is decided to manage some of these forests for game, then dry matter production of the stand as discussed in Section 4.3.6. may be of importance in deciding carrying capacities. However as

stated in the introduction, Nothofagus solandri is one of New Zealand's most important protection forest trees and the primary consideration in the management of the Nothofagus solandri forests must be to keep them in a healthy regenerating condition in order that they effectively act as a barrier to excessive soil erosion and minimise fluctuations in water yield. Introduced browsing mammals almost certainly form the greatest menace to their remaining in a healthy state, and hence the problem of their management has largely become to control these animals at such a level that regeneration can proceed satisfactorily. As the protection forests occupy a considerable proportion of New Zealand's land surface however, economics dictate that control operations cannot be carried out effectively throughout all these forests at present. Consequently priorities must be allocated and one of the main criteria on which the determination of such priorities must depend is the relative susceptibility of the vegetation. Two of the research problems posed on the management of these forests must thus be how to determine which are the ones which are the most susceptible to damage and how to determine whether or not they are satisfactorily regenerating.

The associations of Nothofagus solandri in which regeneration of the forest is at present the most susceptible to damage by animals, are the low complexity ones which occupy large areas on the eastern side of the Main Divide in the South Island, and in the Central North Island. In these forests often the only browse available is seedlings and saplings of the sole canopy tree, Nothofagus solandri. In associations which are more complex the regeneration of Nothofagus solandri may be left untouched, even though it may still be a major,

or even the only large tree species. This is demonstrated by reference to Associations D 1 and B 1. In Association D 1 the mean complexity of vascular plants per plot is just over four species (see Section 3) while in Association B 1 it is nearly 23. In D 1, Nothofagus solandri shows obvious browse in about 30 per cent of the plots where its seedlings or saplings occur within the browse zone, while in B 1 browse is obvious only in about 2 per cent. Broadleaf, most Coprosma species, Pseudopanax species, Polystichum vestitum and a number of other species of plants are preferred to Nothofagus solandri for browse by these animals and until these species are no longer readily available in an association, Nothofagus solandri will probably continue to regenerate itself satisfactorily and it is possible that it may be temporarily aided by removal of competition. Ultimately, however, when alternative browse is no longer plentiful, the regeneration of Nothofagus solandri will become endangered.

Even within the associations of low complexity such as D 1, not all areas are equally susceptible to damage by animals. As the distributional limits of the species are approached the potential for regeneration and growth of Nothofagus solandri becomes reduced.

This can be demonstrated with respect to altitude. Towards bushline seedlings of the species become widely scattered as a result of the reduced seeding, poorer quality of seed, poorer germination rates and greater early mortality rates and the growth of these seedlings becomes very slow. On such sites which are ecologically marginal for survival any added pressure on regeneration such as the introduction of browsing animals must ultimately have a disastrous effect on the survival of the species. These marginal areas for

survival must thus be considered as the most susceptible sites within the associations.

In the associations of low complexity such as D 1, which are the ones which are most susceptible to damage from browsing, advance growth seedlings are naturally held in check by the parent canopy while the basal area of the stand remains above 250 square feet per acre. Once the basal area falls much below this level seedling and sapling growth should rapidly make up the difference. It can be accepted therefore, that a stand of Nothofagus solandri which has a basal area of approximately 250 square feet per acre can be considered to be quite healthy even if no regeneration is present. If, on the other hand, the basal area is considerably less than 250 square feet per acre and there is no sign that seedling growth will make up the difference, then the stand can be considered to be no longer in a healthy and regenerating condition. The application of this relationship between basal area and regeneration and of the seedling ingrowth necessary to maintain the structure of a stand such as is described in Section 4.3.6., must form the most effective basis for deciding whether or not a stand is effectively regenerating and thus whether or not it can be regarded as being in a satisfactory condition.

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APPENDIX 1

A. BOTANICAL NAMES.

Botanical names used in this thesis are according to Zotov (1963) for the grass sub-family Arundinoideae; Cheeseman (1925) for the remainder of the Indigenous Monocotyledones; Philipson (1965) for the genera of the Araliaceae; Hilgendorf and Calder (1960) for the introduced species and Allan (1961) for all remaining species.

B. MEASURES.

In general British Measures have been used. There are two exceptions where the metric scales were used. The first is where Allan (1961) is quoted in the description of the Species, in Sect. 1.2., and the second is in reference to dry weights and leaf areas for the seedling studies in Section 4.2.5. Similar studies on seedlings are nearly always expressed in metric and the switch from the British Scales in this case was dictated by necessity to conform.

APPENDIX 2

SPECIES LIST

Percent frequency or occurrence of all species recorded on the 2400 *Nothofagus solandri* plots

6 percent - 100 percent frequency (actual frequencies given in brackets for each species).

Nothofagus solandri (100), moss (85), Griselinia littoralis (47), Nothofagus menziesii (43), Coprosma parviflora (39), Hymenophyllum spp. (including H. bivalve, demissum, flabellatum, multifidum, pulcherrimum, rarum, revolutum, rufescens, sanguinolentum, villosum) (38), Coprosma pseudocuneata (36), Grammitis billardieri (34), Coprosma foetidissima (33), Phyllocladus alpinus (31), Pseudopanax simplex (31), Myrsine divaricata (29), Podocarpus hallii (29), Polystichum vestitum (28), Uncinia (fine leaved spp.) (27), Pseudopanax crassifolium (25), Astelia (nervosa and trinervia and other large leaved spp.) (24), Nothofagus fusca (24), Cyathodes fasciculata (23), Blechnum minus (22), Uncinia (large leaved spp.) (22), Asplenium flaccidum (20), Carpodetus serratus (19), Coprosma microcarpa (18), Coprosma rhamnoides (18), Rubus cissoides (17), Weinmannia racemosa (17), Coprosma linariifolia (16), Blechnum discolor (15), Blechnum penna-marina (15), Elaeocarpus hookerianus (15), Pseudowintera colorata (15), Cyathodes juniperina (14), Carex spp. (12), Pseudopanax colensoi (12), Blechnum fluviatile (11), Coprosma colensoi (11), Elytranthe spp. (E. colensoi, flavida, tetrapetala) (11), Podocarpus ferrugineus (11), Archeria traversii (10), Blechnum capense (10), Corybas spp. (10), Dacrydium cupressinum

(10), Gahnia procera (10), Gaultheria antipoda (10), Gaultheria depressa (10), Microlaena avenacea (10), Neomyrtus pedunculata (10), Enargea parviflora (9), Metrosideros umbellata (9), Nertera dichondraefolia (9), Libocedrus bidwillii (8), Phymatodes diversifolium (8), Pittosporum spp. (P. anomalum, crassicaule, divaricatum, rigidum) (8), Pseudopanax arboreum (8), Acaena anserinifolia (7), Aristotelia serrata (7), Coprosma ciliata (7), Dacrydium biforme (7), Myrsine australis (7), Podocarpus nivalis (7), Pseudopanax lineare (7), Ranunculus hirtus (7), Fuchsia excorticata (6), Lagenophora petiolata (6), Leptospermum ericoides (6), Leptospermum scoparium (6), Melicytus ramiflorus (6), Pittosporum tenuifolium (6).

5 percent frequency.

Asplenium bulbiferum, Coprosma astonii, Coprosma cheesemanii, Coprosma propinqua, Coprosma robusta, Cyathea dealbata, Dracophyllum longifolium, Dracophyllum traversii, Elaeocarpus dentatus, Hebe vernicosa, Histiopteris incisa, Libertia pulchella, Olearia rani, Parsonsia (capsularis and heterophylla), Phormium colensoi, Poa spp., Pseudopanax anomalum, Quintinia acutifolia, Rubus australis.

4 percent frequency.

Aristotelia fruticosa, Brachyglottis repanda, Coprosma banksii, Coprosma lucida, Coprosma tenuifolia, Cyathea colensoi, Gleichenia cunninghamii, Hypolepis millefolium, Knightia excelsa, Mycelis muralis, Nothofagus truncata, Podocarpus spicatus.

3 percent frequency.

Beilschmiedia tawa, Blechnum lanceolatum, Celmisia spectabilis, Chionochloa conspicua, Clematis paniculata, Clematis spp. (C. afoliata and australis), Coprosma australis, Cyathea smithii, Dacrydium colensoi, Epilobium spp., Hedycarya arborea, Helichrysum glomeratum, Lycopodium fastigiatum, Metrosideros diffusa, Myrsine nummularia, Myrsine salicina, Nertera depressa, Notodanthonia spp., Olearia colensoi, Olearia lacunosa, Podocarpus dacrydioides, Polystichum richardii, Todea hymenophylloides, Trichomanes reniforme.

2 percent frequency.

Aniseotome aromatica, Blechnum vulcanicum, Cardamine debilis, Chiloglottis cornuta, Chionochloa spp. (C. flavescens, pallens, rigida), Dacrydium intermedium, Daniella intermedia, Dicksonia lanata, Dicksonia squarrosa, Dracophyllum uniflorum, Earina (autumnalis and mucronata), Erichtites spp., Gastrodia cunninghamii, Geniostoma liguistrifolium, Grammitis heterophylla, Hebe salicifolia, Hebe stricta, Hypolepis tenuifolia, Luzula spp., Lycopodium volubile, Olearia arborescens, Olearia furfuracea, Oxalis spp., Pittosporum eugenioides, Podocarpus totara, Pteridium aquilinum, Pterostylis spp., Pyrrosia serpens, Rhipogonum scandens, Senecio bennettii, Sophora microphylla, Todea superba, Urtica incisa, Viola filicaulis.

1 percent frequency.

Angelica montana, Asplenium falcatum, Asplenium flabellifolium, Asplenium hookerianum, Asplenium lucidum, Asplenium richardii, Astelia linearis, Chionochloa acicularis, Collospermum hastata, Coprosma crassifolia, Coprosma rotundifolia, Cordyline indivisa,

Coriaria arborea, Corokia cotoneaster, Cyathea medullaris, Cyathodes empetrifolia, Dactylis glomerata, Dracophyllum menziesii, Dracophyllum recurvum, Dracophyllum townsonii, Forstera sedifolia, Freycinetia banksii, Gaultheria crassa, Gaultheria rupestris, Gentiana spp. (inc. G. bellidifolia and spenceri), Geranium microphyllum, Gleichenia circinata, Gymnelaea cunninghamii, Gymnelaea lanceolata, Hebe canterburiensis, Hebe corriganii, Hebe odora, Hebe subalpina, Hebe traversii, Hebe venustula, Helichrysum bellidioides, Helichrysum filicaule, Hoheria glabrata, Hoheria lyallii, Hydrocotyle spp., Hymenanthera alpina, Hymenophyllum malingii, Hypochaeris radicata, Lagenophora pumila, Libertia ixioides, Lophomyrtus obcordata, Lycopodium billardieri, Lycopodium scariosum, Lycopodium varium, Macropiper excelsum, Melicope simplex, Metrosideros fulgens, Metrosideros perforata, Metrosideros robusta,Meuhlenbeckia australis, Muehlenbeckia axillaris, Muehlenbeckia complexa, Olearia avicenniae-folia, Olearia ilicifolia, Olearia nummularifolia, Olearia paniculata, Oreomyrrhis colensoi, Ourisia macrocarpa, Ourisia macrophylla, Paesia scaberula, Parahebe decora, Pellaea rotundifolia, Pennantia corymbosa, Pentachondra pumila, Pittosporum patulum, Pratia angulata, Pseudowintera axillaris, Pseudowintera traversii, Ranunculus lappaceus, Schefflera digitata, Schoenus pauciflorus, Senecio bidwillii, Senecio haastii, Senecio lagopus, Sonchus spp., Thelymitra spp., Thelypteris pennigera, Tmesipteris tannensis, Trifolium spp., Viola cunninghamii, Viola lyallii.

Less than 0.5 percent frequency.

Abrotanella linearis, Acaena novae-zelandiae, Aciphylla sp., Adiantum

sp., Agropyrum scabrum, Agrostis sp., Aira caryophylla, Alectryon excelsus, Alseuosmia macrophylla, Alseuosmia pusilla, Angelica decipiens, Angelica geniculata, Anisotome filifolia, Anisotome haastii, Anisotome pilifera, Anthoxanthum odoratum, Ascarina lucida, Beilschmiedia tarairi, Blechnum filiforme, Blechnum membranaceum, Blechnum nigrum, Blechnum patersonii, Caladenia sp., Carmichaelia grandiflora, Carmichaelia petriei, Carpha alpina, Cassinia fulvida, Cassinia leptophylla, Cassinia vauvilliersii, Celmisia armstrongii, Celmisia coriacea, Celmisia densiflora, Celmisia discolor, Celmisia gracilenta, Celmisia holosericea, Celmisia incana, Celmisia petiolata, Celmisia sessiliflora, Celmisia verbascifolia, Celmisia viscosa, Celmisia walkeri, Cerastium vulgaltum, Chionochloa australis, Chionochloa crassiuscula, Chrysobactron gibbsii, Chrysobactron hookeri, Cirsium spp., Colobanthus sp., Coprosma antipoda, Coprosma areolata, Coprosma brunnea, Coprosma crenulata, Coprosma depressa, Coprosma intertexta, Coprosma petriei, Coprosma pumila, Coprosma rigida, Coprosma rugusa, Coprosma serrulata, Coprosma spathulata, Coprosma tennuicaulis, Coprosma virescens, Cordyline australis, Cordyline banksii, Coriaria lurida, Coriaria plumosa, Coriaria sarmentosa, Cortaderia conspicua, Corynocarpus laevigatus, Cotula spp., Crepis capillaris, Ctenitis decomposita, Ctenitis glabella, Cyathodes colensoi, Cyathodes fraseri, Dacrydium bidwillii, Dacrydium laxifolium, Dendrobium cunninghamii, Deyeuxia sp., Dicksonia fibrosa, Digitalis purpurea, Discaria toumatou, Dodonaea viscosa, Donatia novae-zelandiae, Dracophyllum filifolium, Dracophyllum fiordense, Dracophyllum kirkii, Dracophyllum latifolium, Dracophyllum oliveri, Dracophyllum palustre, Dracophyllum politum, Dracophyllum pyramidale, Dracophyllum subulatum,

Dracophyllum urvilleanum, Drapetes dieffenbachii, Drosera spathulata, Drosera stenopetala, Dysoxylum spectabile, Echinopogon sp., Epacris (alpina and pauciflora), Euphrasia cuneata, Exocarpus bidwillii, Festuca novae-zealandiae, Forstera bidwillii, Forstera tenella, Galium sp., Gaultheria colensoi, Gaultheria oppositifolia, Gaultheria paniculata, Geum parviflorum, Gnaphalium sp., Griselinia lucida, Gunnera strigosa, Gymnelaea montana, Haloragis sp., Hebe elliptica, Hebe gibbsii, Hebe glaucophylla, Hebe hectori, Hebe hulkeana, Hebe macrantha, Hebe parviflora, Hebe pinguifolia, Hebe rupicola, Hebe tetragona, Helichrysum microphyllum, Helichrysum selago, Hemiphues suffocata, Hoheria sexstylosa, Holcus lanatus, Hypericum sp., Hypolepis rugosula, Hypolaena lateriflora, Ixerba brexioides, Juncus sp., Lagenophora pinnatifida, Laurelia novae-zelandiae, Lindsaea trichomanoides, Linum catharticum, Liparophyllum gunnii, Lolium perenne, Lophomyrtus bullata, Loranthus micranthus, Lycopodium australianum, Mazus radicans, Melicytus micranthus, Melicytis ramiflorus, Metrosideros excelsa, Metrosideros parkinsonii, Microtis unifolia, Mida salicifolia, Myoporum laetum, Myosotis sp., Olearia albida, Olearia coriacea, Olearia oporina, Ophioglossum coriaceum, Oreobolus pectinatus, Ourisia caespitosa, Ourisia colensoi, Pachystegia insignis, Parahebe lyallii, Paratrophis microphylla, Pernettya macrostigma, Petriella colensoi, Phormium tenax, Phyllachne colensoi, Phyllocladus glaucus, Phyllocladus trichomanoides, Phymatodes novae-zelandiae, Phymatodes scandens, Pimelia gnidia, Pimela longifolia, Pittosporum colensoi, Pittosporum cornifolium, Pittosporum crassifolium, Pittosporum lineare, Plantago sp., Podocarpus acutifolius, Polystichum cystostegia, Polystichum silvaticum, Pratia macrodon, Prunella vulgaris, Pseudopanax edgerleyi,

Pseudopanax ferox, Pteris macilenta. Quintinia elliptica, Quintinia serrata, Ranunculus insignis, Ranunculus lyallii, Raoulia australis, Raoulia glabra, Raoulia grandiflora, Rhabdothamnus solandri, Rhopalostylis sapida, Rosa eglanteria, Rubus parvus, Rubus schmidelioides, Rubus squarrosus, Rumex acetosella, Rumohra adiantiformis, Rumohra hispida, Schizaea fistulosa, Scirpus sp., Senecio bellidioides, Senecio bifistulosus, Senecio elaegnifolius, Senecio jacobaea, Senecio kirkii, Senecio lautus, Senecio lyallii, Senecio reinoldii, Senecio sexifragoides, Senecio scorzonercides, Sophora prostrata, Stellaria gracilenta, Taraxacum sp., Traversia baccharoides, Tupeia antarctica, Ulex europaeus, Urtica ferox, Wahlenbergia albomarginata, Wahlenbergia gracilis.

APPENDIX 3

PHYSIOGRAPHY AND CANOPY DENSITY FOR EACH OF THE 23 NOTHOFAGUS SOLANDRI ASSOCIATIONS - see Sect. 3

Association	No. of Plots	Canopy Density			Slope				Physiography				
		Open	Mod	Dense	Flat	Gentle	Mod	Steep	Pakihi	Terrace	Gully	Face	Spur
A 1	57	54	28	18	14	33	23	30	45	0	5	31	19
B 1	141	23	38	39	10	31	39	20	0	6	14	42	38
B 2	78	43	29	28	56	36	6	2	72	12	8	3	5
B 3	70	19	40	41	71	18	10	1	79	14	0	4	3
B 4	46	52	29	19	26	27	14	33	50	13	4	22	11
C 1	87	34	45	21	0	20	33	47	0	13	11	40	36
C 2	90	44	35	21	60	20	12	8	47	31	10	6	6
C 3	85	35	29	36	38	26	20	16	0	44	27	15	14
C 4	115	24	50	26	20	32	30	18	0	26	19	23	32
C 5	137	17	34	49	31	27	21	21	0	32	30	19	19
C 6	200	40	28	32	17	29	27	27	0	21	29	22	28
D 1	288	27	30	43	9	26	30	41	0	14	18	35	33
D 2	272	18	31	51	24	24	30	22	12	19	14	29	26
D 3	92	49	24	27	11	23	27	39	10	10	21	37	22
D 4	111	44	29	27	10	22	31	37	0	10	12	41	37
E 1	21	59	31	10	15	24	22	39	0	11	37	35	17
E 2	70	42	32	26	5	12	34	49	0	28	25	32	15
E 3	120	34	36	30	25	32	23	20	0	32	48	16	4
E 4	38	36	36	28	9	27	21	43	0	6	88	6	0
F 1	93	35	50	15	15	29	31	25	0	34	30	16	20
F 2	126	34	36	30	23	18	26	33	0	24	20	10	45
F 3	51	43	23	34	7	25	43	25	0	5	30	20	45
G 1	14	81	12	7	22	0	9	69	0	18	0	27	55

All above figures have been adjusted from the original frequencies to allow for irregular sampling and then expressed as percentages. For example, with the criteria employed for estimating canopy density, there was twice as much chance of a canopy being recorded as having moderate density, than open or dense density. The frequencies were adjusted to allow equal chance for the three possibilities.

APPENDIX 4

Total seed fall and sound seed fall for each line of trays for each collection period.

A. Craigieburn Range. (Date of installation of canisters 16 March 1965).

Year	Collection Date	Line A		Line B		Line C		Line D		Line E	
		Tot	Sound	Tot	Sound	Tot	Sound	Tot	Sound	Tot	Sound
1965	30 Mar	15	-	3	-	1	-	4	-	8	-
	29 Apr	27	-	11	-	6	-	6	-	6	-
	31 May	5	-	4	-	2	1	1	-	1	-
	29 Jun	3	-	4	-	-	-	-	-	-	-
	29 Jul	1	-	3	-	1	-	-	-	-	-
	26 Aug	-	-	-	-	-	-	-	-	-	-
	30 Sep	-	-	-	-	-	-	-	-	-	-
	28 Oct	-	-	-	-	-	-	-	-	-	-
	2 Dec	-	-	-	-	-	-	-	-	-	-
	23 Dec	-	-	1	-	-	-	-	-	-	-
1966	31 Jan	-	-	-	-	-	-	-	-	-	-
	25 Feb	-	-	1	-	16	-	1	-	24	-
	30 Mar	-	-	5	-	186	4	14	-	289	28
	3 May	1	-	12	1	166	40	37	2	183	19
	31 May	1	-	-	-	-	-	-	-	-	-
	30 Jun	-	-	2	-	-	-	3	-	4	-
	1 Aug	-	-	-	-	-	-	-	-	-	-
	29 Aug	-	-	-	-	-	-	-	-	-	-
	26 Sep	-	-	-	-	-	-	-	-	-	-
	3 Nov	-	-	-	-	-	-	-	-	-	-
	6 Dec	-	-	-	-	-	-	-	-	-	-
1967	2 Jan	-	-	-	-	-	-	-	-	-	-
	1 Feb	-	-	-	-	22	-	-	-	2	-
	6 Mar	204	-	368	6	390	15	246	4	32	-
	4 Apr	827	2	790	-	673	17	743	2	778	300
	10 May	1653	181	4221	1610	6710	4490	4836	2332	2386	1170
	1 Jun	51	5	254	57	87	16	121	28	16	-
	4 Jul	40	3	120	15	94	19	63	17	19	5
	1 Aug	8	3	20	2	4	2	8	3	8	4
	20 Aug	2	-	1	-	5	2	6	-	-	-
	4 Oct	-	-	1	-	-	-	-	-	-	-
	1 Nov	1	1	4	-	1	-	1	-	2	-
	6 Dec	4	-	-	-	-	-	-	-	-	-
	28 Dec	1	-	-	-	-	-	-	-	-	-
1968	7 Feb	2	-	-	-	-	-	-	-	-	-
	5 Mar	7	-	30	-	43	-	16	-	1	-
	28 Mar	1	-	5	-	25	-	9	-	2	-
	20 Apr	-	-	-	-	-	-	-	-	-	-

B. Kaweka Range. (Date of installation of canisters 10 March 1965).

Year	Collection Date	Line					
		AA		BB		CC	
		Total	Sound	Total	Sound	Total	Sound
1965	31 Mar	114	-	62	-	25	-
	25 May	11	-	12	-	8	-
	23 Jun	-	-	7	-	2	-
	27 Jul	2	-	4	-	2	-
	14 Sep	-	-	-	-	-	-
	7 Nov	-	-	-	-	-	-
	1 Dec	-	-	-	-	-	-
1966	12 Jan	-	-	-	-	-	-
	16 Feb	-	-	33	-	32	-
	31 Mar	61	-	345	-	831	8
	28 Apr	7	-	61	-	369	8
	31 May	-	-	1	-	13	-
	29 Jun	-	-	-	-	6	-
	3 Aug	-	-	-	-	-	-
	31 Aug	-	-	-	-	-	-
	3 Oct	-	-	-	-	-	-
	1 Nov	-	-	-	-	-	-
	30 Nov	-	-	-	-	-	-
1967	4 Jan	-	-	-	-	-	-
	30 Jan	-	-	-	-	16	-
	28 Feb	24	-	64	-	62	-
	30 Mar	65	2	320	23	221	72
	1 May	5516	942	18838	11176	14915	9042
	30 May	8884	4029	9153	5555	2505	1151
	27 Jun	1489	454	482	181	677	169
	25 Jul	49	18	52	20	64	22
	31 Aug	23	9	103	33	77	14
	28 Sep	7	-	27	2	54	-
	31 Oct	12	-	8	1	3	-
	28 Nov	2	-	26	1	18	3
1968	3 Jan	31	2	36	1	22	-
	1 Feb	10	1	2	-	-	-
	29 Feb	14	-	22	1	18	1
	3 Apr	15	-	18	-	14	1
	30 Apr	-	-	-	-	2	-
	30 May	-	-	-	-	-	-

C. Mt Thomas. (Date of installation of canisters 7 January 1966).

Year	Collection Date	Line F	
		Total	Sound
1966	11 Mar	977	332
	7 Apr	3973	1587
	6 May	1135	194
	2 Jun	193	16
	1 Jul	44	11
	4 Aug	36	8
	31 Aug	9	1
	30 Sep	3	-
	8 Nov	-	-
	7 Dec	-	-
1967	4 Jan	6	2
	1 Feb	-	-
	3 Mar	3	-
	5 Apr	55	15
	10 May	129	14
	29 May	2	-
	3 Jul	9	1
	1 Aug	3	-
	31 Aug	-	-
	30 Sep	-	-
	31 Oct	-	-
	5 Dec	-	-
	26 Dec	-	-
1968	7 Feb	7	-
	5 Mar	5	-
	5 Apr	57	8
	7 May	5	-
	5 Jun	-	-

APPENDIX 5

Record of Past Seed Years in Nothofagus solandri

The following records of seed years refer to Nothofagus solandri alone. Where definite statements of seeding are given, there is substantial supporting evidence in literature that a good or partial seed year did occur in N. solandri for the areas quoted. Where it is stated that seeding was probable for a particular locality, there is written evidence that seeding did occur in at least one of the other species of the 'fusca' group of the genus Nothofagus, and it is assumed that since there is a strong possibility that the climate requirements which stimulate seed production in N. solandri also stimulate seed production in the other species of the 'fusca' group, it is therefore likely that unrecorded seeding also occurred in N. solandri (for detail on this subject see Poole 1955). Where it is stated that possible seeding occurred, the evidence is usually in the form of a general statement without specific reference to species or locality. In all cases the source of information is given.

Year	Extent
1936	Good seed year in the southern North Island, probably extending to Nelson and the central North Island, and possibly occurring throughout the range of the species (Birch 1936, Hocking 1936, Kean and Newcombe unpub. 1937 and Field 1939).
1939	Good seed year in the central North Island. Possibly a good seed year in the southern North Island and Southland (Poole 1948).

1942 Probably partial seed year in North Westland and possibly elsewhere (Smith, 1948, Conway 1952, Poole (no date)).

1945 Probably good seed year in the Reefton area (Conway 1952).

1949 Good seed year in the central and southern North Island, in Canterbury and possibly also in southern Southland. Negligible seed fall in N.W. South Island (Poole 1949, Hocking 1950, Holloway 1949 and N.Z.F.S. files Tuatapere).

1952 Good seed year in N.W. South Island (Conway 1952, Poole 1955 and Kirkland 1958).

1953 Possible seed year in West Otago (Poole 1955).

1954 Good seed year in Southland (N.Z.F.S. files Tuatapere).

1955 Good seed year in central and southern North Island (Elder 1957, Poole 1955, Elder 1959).

1957 Good seed year in Canterbury, parts of Fiordland and probably also in N.W. South Island. Partial seed year in the Tuatapere area. (Kirkland 1958; Riney et al. 1959; Wardle, P. 1961 and N.Z.F.S. files at Tuatapere).

1959 Partial seed year Tuatapere (N.Z.F.S. Tuatapere files).

1960 Partial seed year in parts of Southland and Canterbury, probably also in North Westland (Kirkland 1961, Seed Register F.R.E.S. Rangiora and N.Z.F.S. files Tuatapere).

1963 Partial seed year in central and southern North Island and parts of Southland (N.Z.F.S. files Tuatapere, and own notes).

1966 Good seed year Canterbury foothills and Southland. Partial seed year in North Westland (pers. comm. K. Chandler and P. Allen, own notes).

1967 Good seed year in Canterbury towards Main Divide and in Kaweka Range, central North Island. Probably partial to good seed year throughout most of Main Divide South Island (own notes).

APPENDIX 6

Results of 'Germination and first year seedling development', Trial 'a'. The total number of live germinates for each line of plots (24 square feet) at the time of each count is given. So too is the accumulated germination and accumulated mortality throughout the season.

Year	Date of Count	Line A			Line B			Line C		
		Total	Acc. Total	Acc. Mort.	Total	Acc. Total	Acc. Mort.	Total	Acc. Total	Acc. Mort.
1967	17 Oct									
	25 Oct							175	175	0
	1 Nov				7	7	0	444	448	4
	8 Nov				34	35	1	563	571	8
	15 Nov				34	35	1	563	571	8
	22 Nov				34	35	1	563	571	8
	30 Nov	1	1	0	61	64	3	612	628	16
	6 Dec	0	1	1	69	73	4	623	660	37
	13 Dec	1	2	1	68	94	26	581	662	81
	19 Dec	2	3	1	68	112	44	606	697	91
	28 Dec	2	4	2	68	119	51	605	710	105
1968	3 Jan	2	4	2	73	125	52	609	725	116
	9 Jan	2	4	2	78	134	56	597	728	131
	16 Jan	5	7	2	73	135	62	559	731	172
	23 Jan	2	7	5	51	135	84	439	731	292
	2 Feb	3	8	5	51	139	88	479	783	304
	7 Feb	3	8	5	50	141	91	469	801	332
	16 Feb	2	8	6	48	144	96	433	802	369
	20 Feb	1	8	7	42	147	105	453	826	373
	27 Feb	2	9	7	42	151	109	423	842	419
	5 Mar	3	10	7	37	153	116	390	850	460
	12 Mar	3	10	7	38	157	119	402	873	471
	22 Mar	2	10	8	36	159	123	370	878	508
	28 Mar	2	10	8	35	160	125	357	881	524
	24 Apr	1	10	9	36	165	129	393	922	529
	27 Nov	1	10	9	23	165	142	334	922	588

APPENDIX 7

Results of 'Germination and first year seedling development', Trial 'b'. The total number of live germinates for each treatment (800 seed) at the time of each count is given. So too is the accumulated germination and accumulated mortality throughout the season.

A. Rangiora (150 feet a.s.l.).

Year	Date of Count	Shade 1 Scree Tot.	*A.T.	A.M.	Shade 1 Light subsoil Tot.	A.T.	A.M.	Shade 1 *F.T.S. + L Tot.	A.T.	A.M.	Shade 2 F.T.S. + L Tot.	A.T.	A.M.
1966	20 Sep												
	22 Sep	1	1	0	1	1	0	1	1	0	4	4	0
	26 Sep	1	1	0	7	7	0	3	3	0	8	8	0
	29 Sep	3	3	0	14	14	0	7	7	0	19	19	0
	3 Oct	2	3	1	17	18	1	6	7	1	34	34	0
	6 Oct	2	3	1	23	24	1	5	7	2	76	76	0
	10 Oct	3	4	1	27	28	1	4	8	4	100	100	0
	13 Oct	3	4	1	32	33	1	7	11	4	104	105	1
	17 Oct	3	4	1	34	35	1	8	12	4	115	116	1
	20 Oct	3	4	1	34	36	2	8	12	4	130	131	1
	25 Oct	3	4	1	37	40	3	10	15	5	162	163	1
	27 Oct	2	4	2	37	40	3	9	15	6	177	178	1
	31 Oct	2	4	2	36	40	4	9	15	6	186	187	1
	3 Nov	2	4	2	36	40	4	9	15	6	186	188	2
	7 Nov	2	4	2	36	40	4	10	16	6	194	196	2
	11 Nov	2	4	2	35	40	5	10	16	6	198	200	2
	14 Nov	2	4	2	35	40	5	10	16	6	195	200	5
	17 Nov	2	4	2	35	40	5	10	16	6	192	200	8
	21 Nov	2	4	2	35	40	5	10	16	6	196	204	8
	24 Nov	2	4	2	35	40	5	10	16	6	199	207	8
	28 Nov	2	4	2	35	40	5	10	16	6	197	207	10
	30 Nov	2	4	2	35	40	5	10	16	6	198	208	10
	5 Dec	2	4	2	35	40	5	10	16	6	197	208	11
	8 Dec	2	4	2	35	40	5	9	16	7	199	212	13
	13 Dec	2	4	2	35	40	5	9	16	7	199	212	13
	19 Dec	1	4	3	35	40	5	9	16	7	199	212	13
	22 Dec	1	4	3	34	40	6	8	16	8	198	212	14
1967	1 Jan	1	4	3	34	40	6	8	17	9	200	214	14
	27 Jan	1	4	3	21	40	19	0	17	17	197	214	17
	17 Feb	1	4	3	17	40	23	0	17	17	197	216	19
	1 May	0	4	4	8	40	32	0	17	17	193	216	23

* F.T.S. + L = Forest Top Soil + Litter
A.T. = Accumulated Total
A.M. = Accumulated Mortality

B. Craigieburn (3200 feet a.s.l.).

Year	Date of Count	Shade 2 Light subsoil Tot.	A.T.	A.M.	Shade 2 F.T.S. + Litter Tot.	A.T.	A.M.	Shade 3 F.T.S. + Litter Tot.	A.T.	A.M.	Shade 4 F.T.S. + Litter Tot.	A.T.	A.M.
1966	25 Oct												
	28 Oct				1	1	0						
	3 Nov	1	1	0	4	4	0						
	8 Nov	4	4	0	4	4	0						
	11 Nov	5	5	0	4	4	0	1	1	0			
	15 Nov	4	5	1	4	4	0	1	1	0			
	24 Nov	16	17	1	6	6	0	2	5	3	2	2	0
	28 Nov	15	18	3	11	11	0	4	7	3	4	4	0
	1 Dec	16	19	3	13	13	0	6	9	3	4	5	1
	5 Dec	16	19	3	11	13	2	8	11	3	4	5	1
	8 Dec	16	19	3	11	13	2	8	11	3	4	5	1
	12 Dec	16	19	3	11	13	2	8	11	3	4	5	1
	15 Dec	16	19	3	12	14	2	8	11	3	6	7	1
	19 Dec	16	19	3	12	14	2	8	11	3	7	8	1
	27 Dec	17	20	3	11	14	3	10	13	3	6	8	2
	30 Dec	17	20	3	12	15	3	10	13	3	6	8	2
1967	3 Jan	17	20	3	11	15	4	10	13	3	6	8	2
	5 Jan	17	20	3	11	15	4	10	13	3	6	8	2
	10 Jan	17	20	3	11	15	4	10	13	3	6	8	2
	13 Jan	17	20	3	11	15	4	10	13	3	6	8	2
	30 Jan	17	20	3	11	15	4	10	13	3	6	8	2
	14 Feb	17	20	3	11	15	4	10	13	3	7	9	2
	1 Mar	17	20	3	11	15	4	10	13	3	7	9	2
	15 Mar	17	20	3	11	15	4	10	13	3	7	9	2
	3 Apr	17	20	3	11	15	4	11	14	3	7	9	2
	17 Apr	17	20	3	12	16	4	11	14	3	7	9	2
	3 May	17	20	3	11	16	5	10	14	4	6	9	3

In the remaining treatments which were all in the open (shade 1) the amount of germination was negligible.

C. Craigieburn (4400 feet a.s.l.).

Year	Date of Count	Shade 1 Light subsoil Total	Acc.	Total	Acc.	Mort.	Shade 2 Forest top soil + Litter Total	Acc.	Total	Acc.	Mort.
1966	1 Dec										
	6 Dec	2		2		0					
	9 Dec	3		3		0					
	13 Dec	3		3		0					
	16 Dec	3		3		0					
	19 Dec	3		3		0					
	27 Dec	3		3		0	1		1		0
	29 Dec	3		3		0	2		2		0
1967	3 Jan	3		3		0	2		2		0
	5 Jan	3		3		0	2		2		0
	9 Jan	3		3		0	3		3		0
	13 Jan	3		3		0	3		3		0
	17 Jan	3		3		0	3		3		0
	20 Jan	3		3		0	3		3		0
	24 Jan	3		3		0	2		3		1
	27 Jan	3		3		0	2		3		1
	30 Jan	3		3		0	2		3		1
	2 Feb	3		3		0	2		3		1
	7 Feb	3		3		0	2		3		1
	14 Feb	3		3		0	2		3		1
	1 Mar	1		3		2	5		6		1
	14 Mar	1		3		2	3		6		3
	3 Apr	1		3		2	3		6		3
	18 Apr	1		3		2	3		6		3
	3 May	0		3		3	1		6		5

In the remaining two treatments which were both in the open (shade 1), there was no germination.

APPENDIX 8

Growth increases for Trial 'b' subsection 4.2.5. on Subsequent Seedling Growth and Mortality.

A. Mean Total Weight original and increase (dry weight in gms).

Treatment			Year 1				Year 2			
Site	Shade	Soil	No. of seedlings	Original Weight	Increase	% Inc.	No. of seedlings	Original Weight	Inc.	% Inc.
150	1	A	12	.113	1.867	1651	11	.124	5.939	4804
	2	A	12	.098	1.283	1304	12	.123	6.295	5129
	1	C	12	.113	.268	237	8	.117	1.479	1264
3200	1	A	12	.106	.120	114	12	.116	.637	548
	2	A	12	.104	.107	102	12	.119	.591	498
	3	A	12	.113	.055	48	12	.119	.327	275
	4	A	12	.123	.028	23	12	.123	.238	193
	1	B	12	.119	.369	309	9	.113	.694	586
	1	C	12	.108	.040	37	8	.096	.090	94
	1	D	12	.102	.048	47	9	.119	.046	39
	1	E	9	.121	.003	3	3	.116	.068	58
	2	E	12	.111	.059	53	9	.118	.090	76
4400	1	A	12	.109	.103	94	12	.125	.176	141
	2	A	12	.121	.090	74	12	.116	.388	335
	1	C	12	.115	.055	48	11	.129	.014	11
	1	E	10	.116	-.005	-4	-	-	-	-

Soil A - Forest top soil with litter

B - Forest top soil with coarse litter removed

C - Light [redacted] subsoil

D - Heavy [redacted] subsoil

E - Scree

Shade 1 - Full light

2 - |

3 - | Increasing shade

4 - ↓

B. Mean Root Weight original and increase, including root increase as a percent of total increase (dry weight in gms).

Treatment			Year 1					Year 2				
Site	Shade	Soil	No. of seedlings	Original Weight	Increase	% Inc.	% of total Increase	No. of seedlings	Orig. Weight	Incr.	% Inc.	% of total Increase
150	1	A	12	.042	.621	1463	33.24	11	.046	2.685	5780	45.21
	2	A	12	.038	.470	1226	36.64	12	.046	2.664	5791	42.31
	1	C	12	.042	.171	402	63.52	8	.044	.520	1182	35.17
3200	1	A	12	.040	.060	150	49.79	12	.045	.254	569	39.85
	2	A	12	.039	.063	160	59.09	12	.044	.259	584	43.84
	3	A	12	.043	.036	85	65.86	12	.044	.138	309	42.12
	4	A	12	.046	.023	50	82.54	12	.047	.087	187	36.61
	1	B	12	.044	.148	334	40.19	9	.044	.232	526	33.43
	1	C	12	.041	.051	125	127.54	8	.037	.062	169	69.64
	1	D	12	.040	.049	121	101.39	9	.045	.033	73	73.58
	1	E	9	.045	.025	57	848.15	3	.043	.051	118	74.88
	2	E	12	.042	.049	116	82.60	9	.044	.092	208	102.34
4400	1	A	12	.041	.054	131	52.52	12	.046	.074	161	42.38
	2	A	12	.046	.064	140	71.33	12	.043	.175	404	45.20
	1	C	12	.043	.054	125	97.58	11	.048	.032	150	225.48
	1	E	10	.044	.012	28	-	-	-	-	-	-

C. Mean Shoot Weight original and increase, including shoot increase as a percent of total increase (dry weight in gms).

Treatment			Year 1					Year 2				
Site	Shade	Soil	No. of seedlings	Original Weight	Increase	% Inc.	% of total Increase	No. of seedlings	Orig. Weight	Incr.	% Inc.	% of total Increase
150	1	A	12	.036	.680	1912	36.44	11	.039	2.078	5354	45.21
	2	A	12	.030	.426	1428	33.21	12	.039	2.078	5396	42.31
	1	C	12	.036	.050	139	18.47	8	.037	.390	1061	35.17
3200	1	A	12	.033	.044	132	36.22	12	.036	.221	616	39.85
	2	A	12	.032	.030	93	28.26	12	.038	.184	489	43.84
	3	A	12	.036	.017	49	31.87	12	.038	.103	272	42.12
	4	A	12	.039	.015	39	53.25	12	.039	.073	188	36.61
	1	B	12	.038	.136	360	36.87	9	.038	.294	783	33.43
	1	C	12	.033	.010	30	25.26	8	.029	.036	121	69.64
	1	D	12	.031	.017	55	25.30	9	.037	.032	86	73.58
	1	E	9	.038	.004	12	148.15	3	.037	.019	51	74.88
	2	E	12	.034	.023	68	39.74	9	.037	.014	37	102.34
4400	1	A	12	.034	.035	103	33.82	12	.040	.073	183	42.38
	2	A	12	.038	.018	49	20.32	12	.036	.122	335	45.20
	1	C	12	.036	.019	52	33.84	11	.041	.010	23	225.48
	1	E	10	.036	.008	21	-	-	-	-	-	-

D. Mean Leaf Weight original and increase, including root increase as a percent of total increase (dry weight in gms).

Treatment			Year 1					Year 2				
Site	Shade	Soil	No. of seedlings	Original Weight	Increase	% Inc.	% of total Increase	No. of seedlings	Orig. Weight	Incr.	% Inc.	% of total Increase
150	1	A	12	.035	.566	1613	30.32	11	.038	1.176	3065	19.80
	2	A	12	.030	.387	1278	30.14	12	.038	1.545	4057	24.54
	1	C	12	.035	.048	138	18.01	8	.036	.569	1570	38.48
3200	1	A	12	.033	.017	52	13.99	12	.036	.163	454	25.54
	2	A	12	.032	.013	42	12.65	12	.037	.148	403	25.07
	3	A	12	.035	.001	4	2.28	12	.037	.087	235	26.47
	4	A	12	.038	-.010	-27	-35.80	12	.038	.079	206	32.94
	1	B	12	.037	.085	228	22.94	9	.037	.168	456	24.16
	1	C	12	.033	-.021	-64	-52.80	8	.030	-.008	-28	-9.19
	1	D	12	.031	-.018	-56	-36.70	9	.037	-.019	-52	-42.22
	1	E	9	.038	-.025	-72	-896.30	3	.036	-.002	-6	-2.96
	2	E	12	.034	-.013	-39	-22.49	9	.037	-.016	-44	-17.90
4400	1	A	12	.034	.014	41	13.66	12	.039	.029	74	16.28
	2	A	12	.037	.008	20	8.35	12	.036	.090	251	23.25
	1	C	12	.035	-.017	-49	-31.42	11	.040	-.027	-69	-192.36
	1	E	10	.036	-.025	-68	-	-	-	-	-	-

E. Mean Leaf Number original and increase.

Treatment			Year 1				Year 2			
Site	Shade	Soil	No. of seedlings	Orig. No. of leaves	Increase	% Inc.	No.of seedlings	Orig. No. of leaves	Inc.	% Inc.
150	1	A	12	11.993	143.26	1194	11	13.396	453.42	3385
	2	A	12	10.104	76.06	753	12	13.245	394.76	2980
	1	C	12	11.993	18.09	151	8	12.504	160.12	1281
3200	1	A	12	11.030	9.55	87	12	12.378	74.04	598
	2	A	12	10.875	3.13	29	12	12.757	48.49	380
	3	A	12	12.043	-0.04	-1	12	12.760	22.99	180
	4	A	12	13.252	-1.59	-12	12	13.287	25.55	192
	1	B	12	12.822	31.85	248	9	12.681	93.54	738
	1	C	12	11.301	-2.80	-25	8	9.690	2.43	25
	1	D	12	10.557	-0.31	- 3	9	12.728	0.72	5
	1	E	9	12.967	-5.30	-41	3	12.387	9.28	75
	2	E	12	11.652	-1.24	-11	9	12.720	-0.50	-4
4400	1	A	12	11.456	7.38	64	12	13.536	24.38	180
	2	A	12	12.954	1.21	9	12	12.374	26.13	211
	1	C	12	12.210	-2.21	-18	11	14.070	-5.07	-36
	1	E	10	12.394	-5.39	-44	-	-	-	-

F. Mean Original Leaf Area and Increase in Leaf Area (in sq cm).

Treatment			Year 1				Year 2			
Site	Shade	Soil	No. of seedlings	Orig. area	Increase	% Inc.	No. of seedlings	Orig. area	Inc.	% Inc.
150	1	A	12	2.641	43.429	1645	11	2.785	94.632	3397
	2	A	12	2.308	35.376	1533	12	2.807	133.327	4750
	1	C	12	2.641	3.080	117	8	2.703	33.064	1223
3200	1	A	12	2.461	1.474	60	12	2.668	14.612	548
	2	A	12	2.477	1.238	50	12	2.727	14.755	541
	3	A	12	2.645	1.225	46	12	2.716	11.129	410
	4	A	12	2.828	0.791	28	12	2.811	11.933	424
	1	B	12	2.753	6.768	246	9	2.739	15.564	532
	1	C	12	2.519	-1.427	-57	8	2.340	-0.730	-31
	1	D	12	2.415	-1.070	-44	9	2.744	-1.432	-52
	1	E	9	2.782	-1.972	-71	3	2.667	-0.360	-14
	2	E	12	2.608	-0.418	-16	9	2.687	-0.866	-32
4400	1	A	12	2.538	1.615	64	12	2.836	2.794	99
	2	A	12	2.778	1.520	55	12	2.690	8.883	330
	1	C	12	2.662	-1.085	-41	11	2.900	-1.720	-59
	1	E	10	2.716	-1.856	-68	-	-	-	-

G. Mean Original and Increase in Shoot Length (inches).

Treatment			Year 1				Year 2			
Site	Shade	Soil	No. of seedlings	Original Length	Increase	% Inc.	No. of seedlings	Original Length	Increase	% Inc.
150	1	A	12	2.157	4.026	187	11	2.206	5.827	264
	2	A	12	2.157	3.700	9	12	2.210	11.044	500
	1	C	12	2.006	0.205	184	8	2.177	2.545	117
3200	1	A	12	2.085	0.445	21	12	2.121	1.446	68
	2	A	12	2.082	0.398	19	12	2.200	1.915	87
	3	A	12	2.150	0.221	10	12	2.197	1.060	48
	4	A	12	2.210	0.083	4	12	2.197	0.835	38
	1	B	12	2.200	0.701	31	9	2.193	1.501	69
	1	C	12	2.088	0.028	1	8	1.994	0.619	31
	1	D	12	2.019	0.126	6	9	2.167	0.449	21
	1	E	9	2.206	-0.146	-7	3	2.180	0.315	14
	2	E	12	2.124	0.394	18	9	2.176	0.209	10
4400	1	A	12	2.110	0.453	22	12	2.249	0.552	25
	2	A	12	2.164	0.426	20	12	2.180	1.052	48
	1	C	12	2.163	0.351	16	11	2.262	0.370	16
	1	E	10	2.170	0.126	6	-	-	-	-

APPENDIX 9

Pattern of height growth, on open grown saplings at a number of altitudes in the Craigieburn Range, and at Rangiora, throughout the 1967-1968 growing season. Each figure represents the accumulative mean percentage of the total annual increment which had occurred up to the date of measurement.

A. Craigieburn Range.

	Terminal Growth				Lateral Growth			
Altitude	4400	3900	3200	2700	4400	3900	3200	2700
No. of saplings	10	10	10	10	9	12	12	12
Date of Measure								
30 Aug								
8 Sep								0.17
21 Sep			0.10	0.07		0.26		0.25
27 Sep	0.35	0.19	0.17	0.10	0.32	0.26	0.52	0.33
4 Oct	0.57	0.24	0.28	0.10	0.51	0.52	0.74	1.19
11 Oct	0.57	0.39	0.42	0.33	1.42	1.40	2.50	2.79
20 Oct	1.33	0.85	1.16	0.99	2.20	2.00	4.47	5.59
25 Oct	3.75	2.09	2.13	1.45	4.58	3.64	5.68	9.14
1 Nov	5.29	2.65	2.60	1.89	5.28	4.59	6.22	13.85
8 Nov	5.42	3.10	2.60	2.41	5.85	5.34	6.22	18.52
30 Nov	5.42	3.25	2.77	2.43	5.85	5.34	7.40	19.06
6 Dec	5.42	3.54	8.42	13.50	5.85	5.34	10.19	58.59
13 Dec	5.42	5.62	12.34	16.74	5.85	7.20	16.01	68.08
19 Dec	10.66	12.05	20.82	27.29	8.84	18.70	40.15	81.08
28 Dec	21.40	20.29	25.32	31.52	21.47	33.32	49.84	82.91
3 Jan	34.10	31.12	34.77	35.47	34.28	48.94	64.14	83.90
9 Jan	51.89	46.33	44.37	40.28	50.80	59.58	81.41	84.45
16 Jan	72.03	65.47	52.34	43.55	74.22	82.48	84.49	89.06
23 Jan	80.19	70.61	55.21	46.25	81.08	87.53	85.36	90.03
31 Jan	83.75	71.90	60.50	49.58	82.88	88.76	88.78	91.45
7 Feb	89.98	75.88	64.02	54.97	89.71	91.24	89.00	92.83
14 Feb	91.76	83.84	75.03	64.68	91.13	94.63	89.49	93.30
20 Feb	93.93	84.93	77.21	66.14	91.65	95.86	90.38	93.80
27 Feb	95.55	86.66	82.32	70.54	92.52	96.64	93.30	95.04
5 Mar	96.40	90.76	87.19	73.49	93.56	98.19	93.98	97.02
13 Mar	97.43	93.80	91.37	80.13	95.96	98.85	97.51	98.69
22 Mar	99.43	99.04	97.05	88.26	99.77	99.64	99.69	99.11
28 Mar	100.00	99.50	99.53	95.01	100.00	100.00	100.00	100.00
4 Apr		100.00	100.00	98.54				
23 Apr				100.00				

B. Rangiora.

	Terminal Growth	Lateral Growth
Altitude	150	150
No. of saplings	6	9
Date of Measure		
28 Aug		
4 Sep		1.04
11 Sep		1.10
18 Sep	0.19	1.34
26 Sep	0.34	1.34
2 Oct	0.71	1.89
9 Oct	1.60	4.03
16 Oct	3.51	7.91
24 Oct	6.35	9.17
30 Oct	8.22	11.91
6 Nov	9.82	14.46
13 Nov	11.23	23.67
20 Nov	13.64	33.07
27 Nov	15.12	44.54
4 Dec	16.04	51.59
11 Dec	17.50	53.08
19 Dec	19.72	55.45
26 Dec	20.78	56.98
1 Jan	24.07	58.21
8 Jan	24.89	59.20
15 Jan	27.80	67.36
22 Jan	31.29	69.70
29 Jan	38.37	73.98
5 Feb	44.51	76.54
13 Feb	59.29	80.87
19 Feb	65.23	83.97
26 Feb	71.54	87.37
4 Mar	78.37	91.24
11 Mar	85.49	94.28
18 Mar	91.36	97.16
25 Mar	94.07	98.23
1 Apr	96.71	98.91
8 Apr	100.00	100.00

APPENDIX 10

Litter fall for each line of seed trays for each month during the period of collection. Each figure represents the mean of eight trays converted to lbs. per acre.

A. Leaf Fall.

Year	Month	Line								
		A	B	C	D	E	F	AA	BB	CC
1965	Apr	318.4	444.4	409.5	376.5	259.5	n.r.	321.7	395.5	264.8
	May	141.4	172.7	150.7	127.5	111.1	n.r.	279.8	354.3	241.3
	Jun	88.8	116.6	82.3	64.9	73.9	n.r.	56.3	106.1	90.5
	Jul	12.5	20.6	23.7	16.4	33.0	n.r.	51.9	45.6	51.3
	Aug	20.5	43.5	42.4	26.8	19.2	n.r.	63.5	18.7	33.1
	Sep	49.3	69.2	58.2	61.0	41.8	n.r.	50.8	65.5	50.2
	Oct	53.4	70.3	51.6	63.3	50.4	n.r.	42.9	110.5	68.2
	Nov	54.1	103.2	68.1	36.7	112.3	n.r.	57.0	99.0	144.7
	Dec	110.3	183.1	371.9	148.1	461.6	n.r.	223.8	422.3	438.5
1966	Jan	97.2	169.8	255.7	167.5	325.9	n.r.	247.2	428.1	348.8
	Feb	256.4	238.8	198.8	322.0	427.6	n.r.	358.6	439.4	351.1
	Mar	511.1	456.7	493.0	630.1	287.8	n.r.	581.6	568.4	525.0
	Apr	248.4	296.4	342.6	278.4	341.9	147.4	252.4	369.7	324.6
	May	256.8	260.4	248.7	264.2	200.6	102.5	253.6	274.3	183.4
	Jun	59.6	80.8	99.2	64.0	66.8	61.2	46.1	85.7	63.0
	Jul	24.3	28.3	34.1	20.2	9.3	44.5	63.6	126.6	32.2
	Aug	13.9	15.9	16.9	17.5	13.0	16.9	63.6	45.8	20.3
	Sep	16.6	20.8	26.8	18.5	19.7	8.8	20.0	20.4	12.4
	Oct	19.8	19.8	29.6	20.2	40.7	185.5	42.5	41.8	20.5
	Nov	33.2	51.9	163.5	45.5	229.3	426.3	103.8	158.1	273.9
	Dec	78.0	203.5	436.0	189.5	628.4	509.9	400.3	713.9	585.9
1967	Jan	278.6	414.0	403.2	454.0	410.9	293.5	391.0	460.4	368.2
	Feb	339.9	367.1	386.5	368.9	486.4	128.7	272.3	367.6	263.0
	Mar	374.7	407.7	434.3	379.2	399.7	102.2	365.3	649.3	447.4
	Apr	355.8	492.6	509.1	494.8	410.8	168.1	578.5	662.2	474.7
	May	182.1	261.6	241.0	245.0	231.4	154.7	117.1	176.6	139.9
	Jun	58.5	134.1	99.8	103.6	116.1	135.4	82.7	103.4	91.5
	Jul	25.7	44.8	34.9	27.6	28.4	33.9	14.3	18.0	38.5
	Aug	18.4	15.5	21.0	13.8	5.3	8.3	13.4	6.7	27.4
	Sep	26.0	22.2	28.8	14.6	11.3	2.8	20.3	34.2	36.6
	Oct	20.4	25.3	27.0	23.6	29.3	114.0	11.2	8.9	8.6
	Nov	38.7	55.1	63.1	45.9	105.4	168.0	53.9	144.8	221.1
	Dec	92.5	215.1	225.7	132.4	400.1	393.0	221.1	285.2	401.9
1968	Jan	440.7	668.4	471.2	465.7	447.6	154.9	573.7	494.9	462.5
	Feb	493.9	615.4	402.7	589.9	329.5	121.7	567.7	537.9	357.5
	Mar	178.4	278.0	204.8	181.0	202.9	107.0	165.9	333.3	207.6

n.r. = no record.

B. Twig Fall.

Year	Month	Line								
		A	B	C	D	E	F	AA	BB	CC
1965	Apr	155.3	109.0	98.0	144.0	136.8	n.r.	118.2	165.4	121.1
	May	25.2	54.3	43.0	34.5	33.0	n.r.	110.5	157.4	118.1
	Jun	59.4	59.1	38.0	99.4	19.8	n.r.	68.0	105.5	105.2
	Jul	23.4	35.3	35.5	30.4	51.4	n.r.	94.5	125.6	162.8
	Aug	9.6	37.5	27.0	36.0	14.3	n.r.	75.6	65.3	88.0
	Sep	29.0	56.2	103.8	69.6	57.1	n.r.	69.6	92.2	94.6
	Oct	22.2	40.6	31.9	41.2	45.7	n.r.	68.7	121.5	106.3
	Nov	58.3	113.5	62.8	48.4	156.6	n.r.	45.8	137.7	182.2
	Dec	69.1	284.0	364.6	113.9	99.0	n.r.	37.8	75.0	111.8
1966	Jan	228.4	271.2	167.3	110.0	59.4	n.r.	45.4	95.8	77.5
	Feb	146.4	151.6	60.8	131.2	47.2	n.r.	82.2	116.4	63.6
	Mar	264.4	180.3	122.7	163.0	178.8	n.r.	145.3	153.4	88.2
	Apr	171.1	164.8	129.8	148.9	108.2	83.6	142.8	134.4	196.0
	May	22.7	24.1	19.4	17.3	18.8	29.6	99.6	62.7	68.7
	Jun	31.6	61.6	126.0	89.6	134.8	16.0	15.6	90.2	89.7
	Jul	14.7	35.6	16.2	13.1	1.5	2.9	36.0	55.6	91.4
	Aug	13.5	15.3	7.2	49.8	5.7	44.7	36.0	23.4	43.6
	Sep	9.6	14.2	5.3	30.0	7.0	6.8	22.0	17.2	18.8
	Oct	11.7	9.7	12.6	8.4	11.7	17.1	21.2	13.9	5.3
	Nov	49.8	35. 0	109.2	138.3	126.7	54.1	35.9	28.0	42.2
	Dec	48.5	47.3	51.0	48.7	58.2	47.3	62.0	90.3	115.8
1967	Jan	89.2	103.3	87.5	83.3	145.1	108.6	75.2	94.9	80.9
	Feb	130.2	102.9	101.1	91.5	78.8	57.4	79.1	78.7	54.4
	Mar	148.7	131.0	126.2	114.1	125.3	47.3	148.7	189.1	147.4
	Apr	199.1	241.5	193.5	254.5	248.2	50.8	211.8	298.1	198.0
	May	73.3	91.5	72.5	94.7	75.6	32.9	66.2	97.8	85.4
	Jun	10.0	13.6	10.7	14.5	9.0	23.3	44.2	38.7	60.3
	Jul	15.6	17.2	76.8	25.8	48.2	16.5	35.1	76.5	65.8
	Aug	37.3	24.4	15.2	19.1	12.9	56.9	67.0	22.7	102.5
	Sep	117.8	18.5	43.8	16.1	22.2	0.8	7.0	6.5	9.7
	Oct	45.4	18.2	11.7	23.7	14.1	22.4	3.3	1.9	7.4
	Nov	65.7	70.2	34.0	33.3	97.9	42.5	26.5	29.5	97.9
	Dec	36.0	56.0	55.3	64.7	66.2	59.8	56.8	48.1	54.1
1968	Jan	84.9	128.6	85.9	86.6	132.4	83.6	77.3	61.8	67.1
	Feb	206.3	259.5	157.9	180.2	76.5	43.2	107.8	84.0	67.8
	Mar	83.7	133.8	78.1	104.8	44.5	22.3	88.7	102.8	78.7

n.r. = no record.

APPENDIX 11

Height growth from stem analysis of trees from the Craigieburn Range.

Height (in)	3000 feet			4400 feet		
	No. of Trees	Mean Age	S.E. P=0.05	No. of Trees	Mean Age	S.E. P=0.05
54	10	24.9	6.2	10	16.4	8.8
120	10	39.0	6.2	10	34.0	11.2
240	10	61.9	17.3	10	62.1	13.5
360	10	75.8	17.8	10	110.5	32.6
480	10	96.3	22.6	10	163.5	52.1
600	8	126.4	34.7			
720	7	154.3	44.7			
840	4	193.5	93.8			
	Stand Top Height 870 in.			Stand Top Height 535 in.		

APPENDIX 12

Radius breast height growth, from stem analysis of trees from the Craigieburn Range.

Age	3000 feet			4400 feet		
	No. of Trees	Mean radius B.H. (in.)	S.E. P = 0.05	No. of Trees	Mean radius B.H. (in.)	S.E. P = 0.05
10	10			10	0.06	0.15
20	10	0.03	0.06	10	0.27	0.33
30	10	0.20	0.22	10	0.71	0.54
40	10	0.53	0.45	10	1.30	0.87
50	10	1.01	0.59	10	1.68	1.00
60	10	1.40	0.65	10	2.12	1.04
70	10	1.77	0.64	10	2.51	1.02
80	8	2.17	0.64	10	2.88	1.00
90	8	2.58	0.60	10	3.21	1.04
100	8	2.95	0.61	9	3.57	1.08
110	8	3.27	0.64	9	3.97	1.04
120	8	3.59	0.66	8	4.32	1.04
130	8	3.96	0.68	5	4.69	1.20
140	7	4.34	0.71	5	5.21	1.43
150	7	4.80	0.72	5	5.68	1.51
160	7	5.14	0.84	5	6.15	1.56
170	6	5.65	0.97	5	6.54	1.61
180				5	7.01	1.68
190				5	7.42	1.67
200				5	7.81	1.62
210				5	8.26	1.61
220				5	8.60	1.57
230				4	9.09	1.75
240				4	9.50	1.75

APPENDIX 13

Main trunk volume growth (in cubic feet) from stem analysis of trees from the Craigieburn Range.

Age	3000 feet			4400 feet		
	No. of Trees	Mean Volume	S.E. P = 0.05	No. of Trees	Mean Volume	S.E. P = 0.05
10	10	0.0001	0.0002	10	0.0067	0.0120
20	10	0.0044	0.0052	10	0.0489	0.0706
30	10	0.0337	0.0438	10	0.1882	0.2125
40	10	0.1311	0.1601	10	0.5446	0.5347
50	10	0.3760	0.3379	10	0.9204	0.8120
60	10	0.8083	0.6908	10	1.4998	1.2967
70	10	1.4468	1.1771	10	2.1261	1.5278
80	8	2.3365	2.0448	10	2.9628	1.8700
90	8	3.6148	2.9386	10	3.9749	2.4244
100	8	4.9798	3.5846	9	4.9815	2.8919
110	8	6.5204	4.1920	9	6.3859	3.1863
120	8	7.9344	4.8171	8	7.8074	3.7919
130	8	9.7377	5.2727	5	8.0793	4.2951
140	7	12.1058	6.0885	5	10.1996	5.5407
150	7	15.5637	6.8089	5	12.2973	6.6744
160	7	18.6413	7.9108	5	14.7389	7.6544
170	6	23.1753	9.9555	5	17.0372	8.4419
180	2	31.4448		5	19.7475	9.2708
190	2	36.9559		5	22.4572	9.8139
200	2	43.5543		5	26.1527	12.0639
210				5	29.5345	12.7046
220				5	32.3489	13.0609
230				4	35.7182	15.7689

APPENDIX 14

Volume Table Nothofagus solandri (in cubic feet).

Diam. Class	Height Class						
	10	20	30	40	50	60	70
1.0	0.1	0.2					
2.0	0.2	0.3	0.4				
3.0	0.3	0.5	0.7	0.9			
4.0		1.0	1.3	1.6			
5.0		1.6	2.2	2.8	3.4		
6.0		2.3	3.2	4.1	5.0		
7.0		3.0	4.3	5.6	6.9	8.2	
8.0		3.8	5.6	7.4	9.2	11.0	
9.0		4.8	7.2	9.5	11.9	14.2	16.6
10.0		6.0	8.9	11.7	14.6	17.4	20.2
11.0		7.4	10.7	14.0	17.3	20.6	23.9
12.0		8.9	12.7	16.4	20.1	23.9	27.7
13.0		10.6	14.8	19.0	23.3	27.5	31.8
14.0		12.4	17.1	21.9	26.7	31.4	36.2
15.0		14.2	19.6	25.0	30.4	35.8	41.2
16.0		16.3	22.3	28.3	34.3	40.3	46.3
17.0			25.1	31.7	38.3	44.9	51.5
18.0			28.0	35.3	42.5	49.8	57.0
19.0			30.9	38.9	46.9	54.9	62.9
20.0			33.8	42.6	51.4	60.2	69.0
21.0			36.7	46.5	56.3	66.1	75.9
22.0			39.6	50.5	61.5	72.4	83.4
23.0			42.6	54.8	67.0	79.2	91.4
24.0			45.6	59.3	73.0	86.7	100.4
25.0			48.7	64.1	79.5	94.9	110.3
26.0			51.8	69.2	86.5	103.8	121.2
27.0			54.0	73.7	93.4	113.1	132.8
28.0			57.3	80.5	103.7	126.9	150.1

No. Samples = 296 (From 20 Stem analysis)
Aggregate difference % = 0.2%
Average % Cell Deviation = 6.8% ; (taking sign into account) = 0.4%

APPENDIX 15

Derivation and Use of Index of Similarity I' (see page 75)

The formulae for this index is

$$I = \frac{100\ (15d + 6p + s)}{15d + 6p + s + 3a} \qquad \text{- - - - - - (1)}$$

where d = number of species dominant in both of two plots being compared

p = number of species above 'seedling only' status present in both plots but not present as a dominant in more than one of them

s = number of species present in both plots but occurring as a 'seedling only' in at least one of them

a = number of species present in one only of the plots being compared.

The basic form of this index is similar to Sorensen's K (see pp 77)

$$\text{Sorensen's K} = \frac{100\ (2c)}{x + y} \qquad \text{- - - - - - (2)}$$

where c <u>can</u> = sum of species common to both plots being compared (i.e. d + p + s) of Formulae (1))

x and y <u>can</u> = the total number of species in each of the two plots respectively (i.e. 2 (d + p + s) + a of Formulae (1)).

By substitution of d, p, s and a for c, x and y, Sorensens K becomes $\frac{2 \times 100\ (d + p + s)}{2\ (d + p + s) + a}$

or $\frac{100\ (2d + 2p + 2s)}{(2d + 2p + 2s) + a}$.

The final form of the index of similarity I which is

$$I = \frac{100\ (15d + 6p + s)}{15d + 6p + s + 3a}$$

was arrived at by assigning arbitrarily chosen weightings to the physiognomic status of species in common to the two plots being compared. The weightings of 15 : 6 : 1 attached respectively to d, p and s were chosen so as to give a ratio of importance of approximately 5 : 3 : 1 (see pp 81) for comparisons of plots of mean complexity and mean similarity for the study. The ratio of importance of 5 : 3 : 1 is not constant though, and as the species composition of the plots being compared approaches identity the ratio approaches 1 : 1 : 1. Conversely, as the plots become more dissimilar, dominants in common gain relatively more importance and the ratio approaches 15 : 6 : 1. The complexity of the plots being compared also has an influence on the relative weighting. Where the floristic complexity of the plots is simple, weighting towards dominance is less than where greater numbers of species are encountered.

The weighting of 3 on 'a' was chosen to spread the range of 'I' encountered in the study more regularly between 0 and 100. If a smaller weighting for 'a' had been chosen, then 'I' would tend to be grouped near 100, while if a larger weighting had been chosen, 'I' would have tended to have been grouped towards zero.